Review

Reciprocal relations between cognitive neuroscience and formal cognitive models: opposites attract?

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Cognitive neuroscientists study how the brain implements particular cognitive processes such as perception, learning, and decision-making. Traditional approaches in which experiments are designed to target a specific cognitive process have been supplemented by two recent innovations. First, formal cognitive models can decompose observed behavioral data into multiple latent cognitive processes, allowing brain measurements to be associated with a particular cognitive process more precisely and more confidently. Second, cognitive neuroscience can provide additional data to inform the development of formal cognitive models, providing greater constraint than behavioral data alone. We argue that these fields are mutually dependent; not only can models guide neuroscientific endeavors, but understanding neural mechanisms can provide key insights into formal models of cognition.

Introduction

The past decade has seen the emergence of a multidisciplinary field: model-based cognitive neuroscience [1–7]. This field uses formal cognitive models as tools to isolate and quantify the cognitive processes of interest, to associate them with brain measurements more effectively. It also uses brain measurements such as single-unit electrophysiology, magnetoencephalography, electroencephalography (EEG), and functional magnetic resonance imaging (fMRI) to address questions about formal models that cannot be addressed from within the models themselves.

Figure 1 presents a schematic overview of the relation between three different fields that all study human cognition: experimental psychology, mathematical psychology, and cognitive neuroscience. These disciplines share the common goal of drawing conclusions about cognitive processes, but each branch has a distinct approach; experimental psychologists focus on behavioral data, mathematical psychologists focus on formal models, and cognitive neuroscientists focus on brain measurements. The figure also illustrates how the 'model-in-the-middle' approach [1] can unify these separate disciplines by using a formal model as the pivotal element to bridge behavioral data and brain measurements with estimates of pertinent cognitive processes. By their nature these cognitive processes are latent; that is, they are hypothetical and must be inferred from data. Examples of latent cognitive processes include memory encoding, response caution, response inhibition, and conflict monitoring.

This review focuses on one particular element of the model-in-the-middle approach: the symbiotic relationship between cognitive modeling and cognitive neuroscience (Figure 1, red arrow). We begin by outlining the benefit of using formal cognitive models to guide the interpretation of neuroscientific data, a practice that has a relatively long history in vision sciences [8–10] but is increasingly used to formulate linking propositions of increasing complexity. We then discuss the equally important issue of using neuroscientific data to inspire and constrain cognitive models, which is crucial when competing cognitive models cannot be discriminated solely on the basis of behavioral data [7,11,12]. Throughout the review we highlight recent studies that exemplify the interaction between formal cognitive models and cognitive neuroscience. The conclusions from some of these individual studies will be refined by future research efforts; what is important here is that the studies under consideration combine formal cognitive models and cognitive neuroscience, demonstrating the recent trend towards increased integration of the two research fields.

We conclude that the relationship between cognitive modeling and cognitive neuroscience results in progress towards the shared goal of better understanding of the functional architecture of human cognition. This relationship will accelerate the search for mechanistic explanations of cognitive processes and will discourage the assignment of cognitive functions to particular neural substrates without first attempting to disentangle the myriad operations that underlie a single behavioral output measurement such as response time or accuracy.

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 1364-6613/$ – see front matter © 2011 Elsevier Ltd. All rights reserved. doi:10.1016/j.tics.2011.04.002

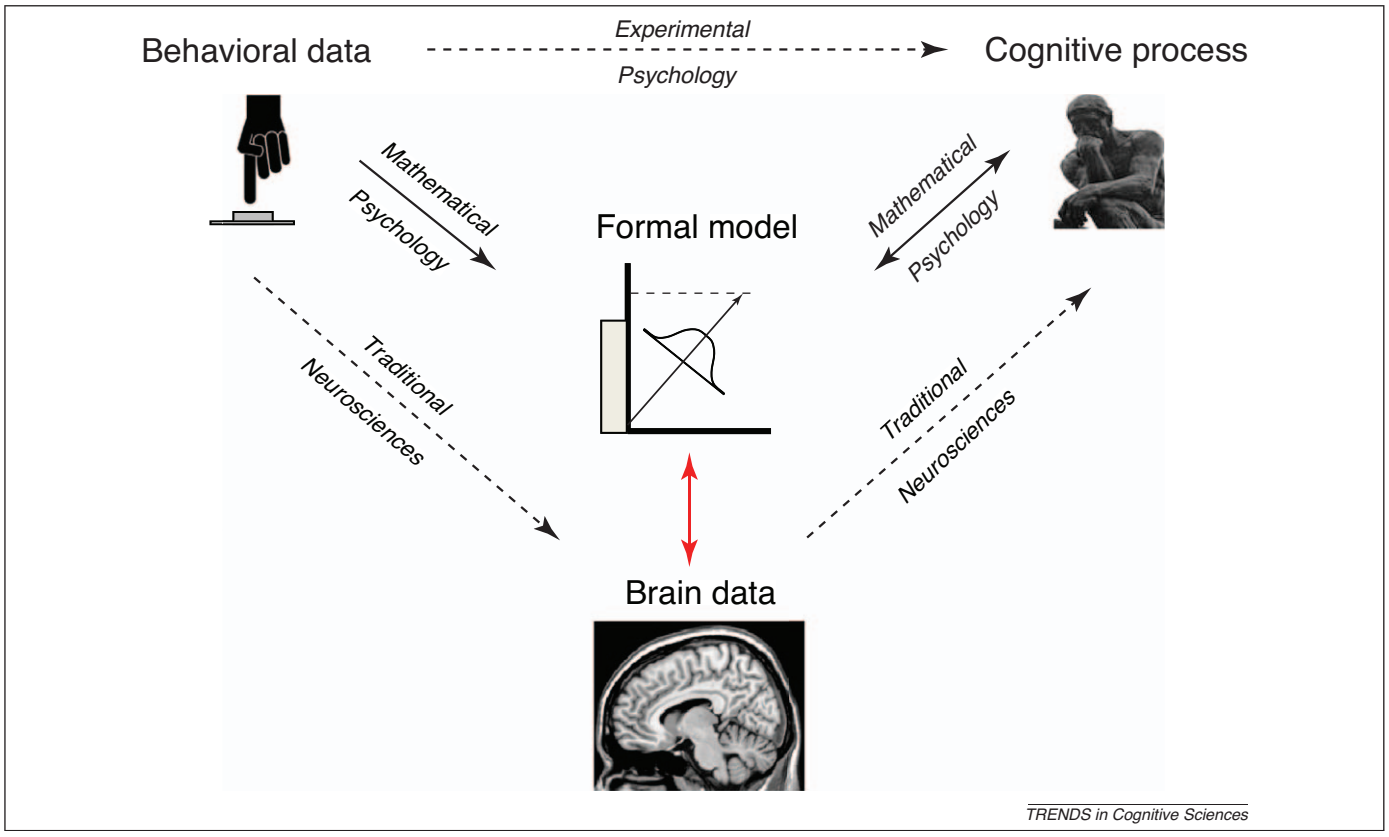

Figure 1. The 'model-in-the-middle' paradigm [1] unifies three different scientific disciplines. The horizontal broken arrow symbolizes experimental psychology, which studies cognitive processes using behavioral data; the diagonal broken arrows symbolize cognitive neuroscience, which studies cognitive processes using brain measurements and constraints from behavioral data; the top two arrows symbolize mathematical psychology, which studies cognitive processes using formal models of cognitive processes constrained by behavioral data. The bidirectional red arrow symbolizes the symbiotic relationship between formal modeling and cognitive neuroscience and is the focus of this review.

Formal cognitive models

Formal models of cognition come in widely differing shapes and sizes. Depending on the goal of the researcher, the behavior under study, and the preferred level of explanation, formal models of cognition range from the simple to the complex; from the specific to the general; from the superficial to the profound; and from the mathematical to the computational. For example, signal-detection theory [13] converts hits (i.e. correct identifications of a target item, such as when a studied picture is correctly classified as 'old') and false alarms (i.e. incorrect identification of a distractor item, such as when a non-studied picture is erroneously classified as 'old') to measures for bias and discriminability. This model is simple, relatively general, superficial (in the sense that it stays very close to the observed data), and mathematical (in the sense that no computer is needed to apply the model). At the other extreme, a model such as ACT-R [14,15] uses IF–THEN production rules to solve reasoning tasks by retrieving and updating information stored in memory. Compared to signal-detection theory, ACT-R is complex, general, profound, and computational.

Although formal models of cognition differ in many dimensions, they all use observed behavior to infer something about an underlying cognitive process. Table 1 lists ten formal models, the different domains in which they are

Table 1. Ten formal models of cognition, their main domain of application, examples of associated cognitive processes, and key references

Model	Domain	Cognitive processes	References
ACT-R	General	Reasoning, arithmetic	[14]
BART-M	Risky decision making	Risk-taking propensity	[62]
DDM	Fast decision making	Caution, bias, ability	[63]
EV	Reinforcement learning	Response consistency	[23]
GCM	Perceptual categorization	Selective attention	[64]
LBA	Fast decision making	Caution, bias, ability	[18]
MPT	General	Retrieval, guessing	[65,66]
PDP	Memory	Recollection, familiarity	[67,68]
PT	Deliberate decision making	Loss aversion	[69–71]
REM	Memory	Storage	[72,73]

Many more models exist, but few have been applied in the neurosciences. ACT-R, adaptive control of thought–rational; BART-M, balloon analogue risk task model; DDM, drift diffusion model; EV, expectancy-valence model; GCM, generalized context model; LBA, linear ballistic accumulator; MPT, multinomial processing tree models; PDP, process dissociation procedure; PT, prospect theory; REM, retrieving effectively from memory.

applied, and the cognitive processes that they attempt to estimate. An exhaustive list of formal cognitive models would be very long and our selective list of ten includes only those models that are particularly prominent or discussed later in this article. As can be seen from Table 1, some models are from the same domain and estimate the same cognitive processes (e.g. the linear ballistic accumulator [LBA] model and the drift diffusion model); these models can be thought of as either competing theoretical accounts (but see [16]) or as complimentary measurement tools. In other cases, the models may be general (e.g. ACT-R and multinomial processing tree models) but the modeling tradition might be fundamentally different. Most often, different models describe different behaviors using different mechanisms and processes (e.g. cumulative prospect theory and the generalized context model).

Regardless of their variety, any particular formal model must be subjected to several sanity checks before it is applied in scientific practice. These sanity checks are required to provisionally conclude that the model's parameters are reliable and veridical reflections of hypothesized latent cognitive process (Figure 2). Only when this is the case can there exist a symbiotic relationship between formal cognitive models and cognitive neuroscience.

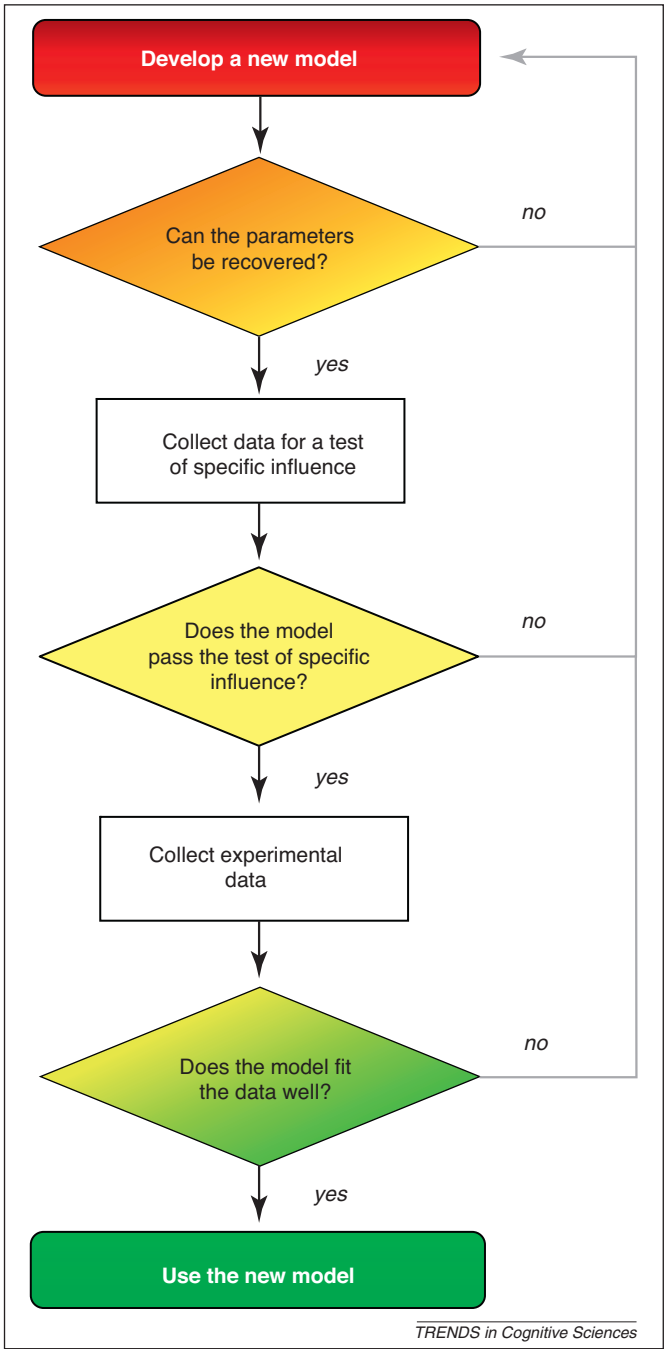

Figure 2. Flowchart for the assessment of model validity. First, simulation studies must confirm that the model can recover known parameter values used to generate synthetic data of realistic length. Failure to recover these values suggest that the model needs to be simplified (i.e. parameters must be eliminated) or additional data need to be collected [74]. Second, a test of specific influence must verify that the model parameters correspond uniquely to the hypothesized cognitive processes [52]. For example, instruction to respond more or less carefully should affect only the parameter that corresponds to response caution. Third, the model must fit the data well. Failure to do this suggests that the estimated parameters do not accurately reflect the corresponding cognitive processes. Moreover, a good fit must be achieved with relatively few degrees of freedom; this usually means that parameters are constrained across experimental conditions in a meaningful way [16].

How formal models inform cognitive neuroscience

Once a model has been validated, it can be used to inform cognitive neuroscience in several ways.

First, formal cognitive models decompose observed behavior into constituent cognitive components and thereby provide predictors that allow researchers to focus more precisely on the process of interest and attenuate the influence of nuisance processes [17]. In this capacity, cognitive models help to enhance sensitivity in the analysis of neuroscientific data, thereby allowing more specific inferences. For example, the LBA model [18] decomposes response choice and response time into meaningful cognitive concepts such as the time needed for peripheral processes (e.g. encoding the stimulus, executing the motor response), response caution, and the speed of information processing. This model-based decomposition was exploited in a recent experiment on the neural mechanisms of response bias [19]; see also [20]. In this experiment, participants had to decide quickly whether a random dot kinematogram was moving left or right [21]. Before the onset of the stimulus, a cue provided probabilistic information about its direction, intended to bias the participant's decision; for example, the cue 'L9' indicated that the upcoming stimulus was 90% certain to move to the left. The behavioral data confirmed that prior information biased the decision process; actions consistent with the cue were executed quickly and accurately, and actions inconsistent with the cue were executed slowly and inaccurately. The LBA model accounted for these data by changing only the balance between the response caution parameters for the competing accumulators. Despite the cue-induced bias being clearly visible in the behavioral data, and the model fitting the observations, fMRI data did not reveal any reliable cue-induced activation. However, the inclusion of a response bias measurement – estimated from the LBA parameters – as a covariate in the regression equation revealed cue-related activation in regions that, in most cases, matched the theoretical predictions (e.g. putamen, orbitofrontal cortex, hippocampus). This result suggests that, by increasing corticostriatal activation, the human brain uses prior information to selectively disinhibit preferred responses.

More generally, this example highlights the practical benefits of using a formal model to simultaneously increase the specificity of inferences made about underlying cognitive processes and the sensitivity of neuroscientific measurements.

Second, formal cognitive models allow researchers to identify the latent process that is affected by their experimental manipulation, in either a confirmatory or an exploratory manner. For example, Sevy et al. [22] used the expectancy-valence model for the Iowa gambling task [23]; this task is complex and probably involves many cognitive operations that are often not explicitly dissociated when neuroscientific measurements are recorded. However, the application of a formal model allowed the task to be decomposed into separable latent variables, permitting Yechiam et al. to argue that a reduction in dopaminergic activity selectively increased the model's recency parameter. This finding reveals substantially more than the general statement that dopaminergic depletion impairs overall performance; instead, it specifically supports the hypothesis that low dopaminergic activity enhances

Box 1. Case study

The subjective value of a stimulus has long been known to bias behavioral choice, and neuroscientific investigations over the past decade suggest that value directly modulates the operation of the sensorimotor neurons that guide motor interactions with the environment. Following the approaches employed by these early single-unit recording studies, Serences used a combination of linear-nonlinear-Poisson (LNP) models and logistic regression models (based on [54–58]) to show that the subjective value of a stimulus also modulates activation levels in areas of the early visual cortex (e.g. V1, V2) that are typically thought to play a primary role in representing basic low-level sensory features (as opposed to regions more directly involved in mediating motor responses [75]). The implication of this observation is that reward influences not only late-stage response thresholding mechanisms, but also the quality of the sensory evidence accumulated during decision making.

More importantly, the computational models that were employed provided trial-by-trial estimates of the subjective (and latent) value assigned to each of two stochastically rewarded choice alternatives based on the prior reward and prior choice history of each option (Figure I). These trial-by-trial estimates open up several analysis alternatives ranging from within-subject sorting of trials into several discrete bins based on the subjective value of the selected alternative [54,56], to evaluation of the continuous mapping between value and neural responses. This ability is crucial because the strategies employed by individual subjects vary [58], and thus within-subject estimates are inherently more sensitive than simply comparing the values of two stimulus classes on a between-subject basis. In the case of reward-based learning, some subjects heavily weight recent rewards while disregarding past rewards, and thus are fast to adapt to transitions in reward probability at the expense of choice stability. Other subjects employ a much longer integration window that trades-off improved stability for decreased flexibility to adapt as reward ratios change over time. These formal models may provide a powerful tool to classify reward sensitivity (and many other cognitive factors of interest) on a within-subject basis, thereby opening up new avenues of clinical inquiry. For example, a predilection for overweighting recent rewards might be associated with traits such as impulsivity [76]. Thus, the use of relatively simple computational models can reveal how individuals represent latent cognitive factors, providing a powerful tool for gaining insights into both normal and abnormal behavioural tendencies and their underlying neural mechanisms.

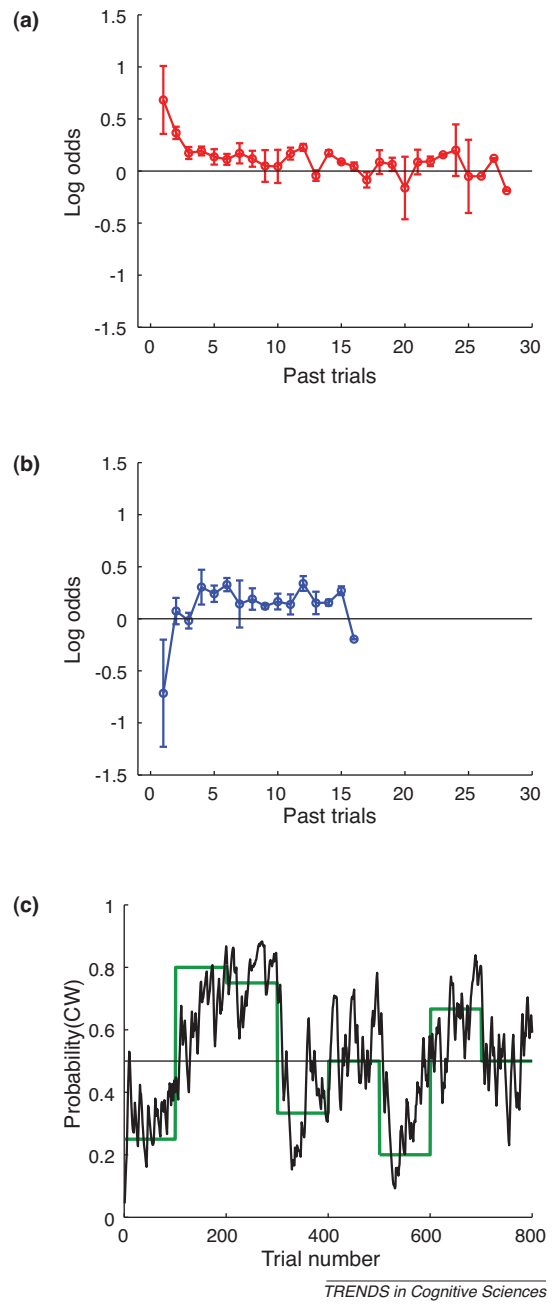

Figure I. **(a)** Influence of rewards earned *n* trials in the past on the log odds of choosing one of two options in the current trial (a clockwise or counter-clockwise rotated grating), where each option was stochastically rewarded at an independent rate. **(b)** Similar to A, but depicts influence of prior choices on current choice; a prior choice decreases the probability of the same choice being made in the current trial because the task included a 'baiting' scheme to encourage switching between alternatives [54,55,57,58]. **(c)** Estimated influence of prior rewards and choices **(a, b)** can be combined to generate a trial-by-trial estimate of the probability that one of the options will be selected (in this case, the probability of the clockwise grating being selected is shown by the black line after the application of a causal Gaussian filter to smooth the data [57,58]. The green line depicts the expected choice probabilities for each block of trials based on the relative reward probability assigned to each choice alternative. For this subject, the estimated choice probability (black line) closely tracked the expected probabilities, supporting the notion that the estimated choice probability can serve as a stand-in for the subjective value of each alternative. Note, however, that there are local trial-by-trial fluctuations away from the expected choice probabilities, consistent with momentary changes in the subjective value of an option given the stochastic reward structure of the task. Data based on [58].

attention to recent outcomes at the expense of outcomes obtained in the more distant past.

Third, formal cognitive models can be used to associate patterns of brain activation with individual differences in cognitive processes of interest. For example, in an fMRI experiment on the speed–accuracy trade-off, Forstmann et al. [24] found that instructions to respond quickly resulted in focused activation of the right anterior striatum and the right pre-supplementary motor area (pre-SMA). Application of the LBA model to the behavioral data revealed that the effect of speed instruction was to selectively lower the LBA response caution parameter. However, speed instructions affected some participants more than others, and participants who had a relatively large decrease in LBA-estimated response caution also showed a relatively large increase in right anterior striatum and right pre-SMA activation. This example illustrates how an individual difference analysis can increase confidence in the association between a particular cognitive process and activation in a specific brain network [25].

Fourth, formal cognitive models can directly drive the principled search for brain areas associated with a proposed cognitive function. This approach has been used successfully in the field of reinforcement learning, which is one of the earliest applications of model-based cognitive neuroscience [2,6,26–28]. In fMRI research, this means that a formal cognitive model is designed to make predictions that are then convolved with the hemodynamic response function. Next, the predicted blood oxygenation level dependent signal (BOLD) response profiles are used to search for areas of the brain with similar activation profiles. For example, Noppeney et al. [29] used the compatibility bias model for the Eriksen flanker task [30] to generate predicted BOLD response profiles to locate a brain region involved in the accumulation of audiovisual evidence. A similar but more confirmatory approach was taken by Borst et al. [31], who used the ACT-R model to predict hemodynamic responses in five brain regions, with each region corresponding to a cognitive resource in the model [14,32,33]).

In summary, there are many ways in which cognitive models have informed cognitive neuroscience. There is no standard procedure and the single best way to proceed depends on the model, the brain measurement technique, and the substantive research question. Although the above examples focus primarily on fMRI studies, the general principles apply regardless of the measurement technique (see [34] for an application involving EEG), and can be used to gain insight into the relationship between latent processes and neural mechanisms on both within- and between-subject bases (at least with data from humans, Box 1).

How cognitive neuroscience informs cognitive models

Until a few years ago, neuroscientific data played a modest role in constraining cognitive models and guiding their development (with the exception of neurocomputational models specifically designed to account for neural data [35,36]). One example of a prominent cognitive model that has undergone a transformation as a result of neuroscience data is ACT-R [14,32,33], in which particular brain areas are now associated with separate cognitive modules, thereby placing severe constraints on the model. For example, if a task is found to evoke activity in a certain area of the posterior parietal cortex, the ACT-R model is constrained to employ the 'imaginal module' to account simultaneously for the observed behavior and the BOLD response. The specific subdivision of cognitive modules in the ACT-R model was informed by the neuroscience data [14,32,33]).

In general, brain measurements can be viewed as another variable to constrain a model or select between competing models that could not otherwise have been distinguished [6,7]. For example, two competing models may have fundamentally different information processing dynamics but nonetheless generate almost identical predictions for observed behavior. When brain measurements can be plausibly linked to the underlying dynamics, this provides a powerful way to adjudicate competing models. We illustrate this approach with three closely related examples.

Churchland et al. [37] studied multi-alternative decision making in monkeys using single-cell recordings. Monkeys performed a random dot discrimination task (Box 2) with either two or four response alternatives. Mathematical models of multi-alternative decision making such as the LBA (Box 2) often assume that when the number of choice alternatives increases, participants compensate for the concomitant increase in task difficulty by increasing their response caution; that is, by increasing the distance from starting point to response threshold [38]. However, behavioral data cannot discriminate between a decrease in starting point and an increase in response threshold, and in the formal models these mechanisms are conceptually distinct but mathematically equivalent. The results of Churchland et al., however, support the decrease-in-starting point

Box 2. Outstanding questions

- How can we apply our knowledge from formal models and cognitive neuroscience to psychiatric and neurological disorders [59]? Can parameters from cognitive models provide endophenotypes that are more sensitive and specific than those based on observed behavior?
- What are the benefits for cognitive neuroscience when relatively abstract cognitive models are combined with more concrete neurocomputational models? As the fields of cognitive neuroscience and cognitive modeling grow closer, abstract models should ideally start to incorporate assumptions about the neural substrate.
- Can we carefully validate the linking hypotheses that relate neuroscientific data to the formal cognitive models? These linking hypotheses are important for drawing valid conclusions from data, and they are often also interesting research questions in their own right.
- Can we strengthen our inferences through development of integrated approaches that combine data-driven cognitive neuroscience with cognitive modelling techniques? Initial work with analysis methods such as ancestral graph theory [60] and single trial estimation based on multivariate decomposition [61] point in this direction.
- What are the benefits for cognitive neuroscience when mixture models are used to classify participants or trials into separate categories? This approach could, for example, be applied to allow the probabilistic identification of task-unrelated thoughts (TUTs); that is, trials on which the participant experiences a lapse of attention.

account and not the increase-in-threshold account; in the four-alternative task, neural firing rates in the lateral intraparietal area started at a relatively low level but finished at a level that was the same as that in the two-alternative task.

A second example comes from Ditterich [11], who compared a range of formal models for multi-alternative perceptual decision making. All of the models integrated noisy information over time until the response threshold, but they differed in many other important aspects: information was integrated with or without leakage, competition between accumulators was accomplished by feedforward or feedback inhibition, and accumulator output was combined across alternatives by linear or nonlinear mechanisms. After fitting the models to the data, Ditterich concluded that 'it seems to be virtually impossible to discriminate between these different options based on the behavioral data alone'. However, this does not mean that the models cannot be discriminated at all. In fact, Ditterich demonstrated that the internal dynamics of the models have unique signatures that could be distinguished – at least in principle – using neurophysiological data [37]).

A third example comes from Purcell et al. [39], who used a speeded visual search task in which monkeys were required to make an eye movement toward a single target presented among seven distractors. They measured single-cell firing rates in visual and movement neurons from the frontal eye field (FEF) in an attempt to distinguish various accumulator models for evidence integration and decision. Constraint for the models was gained by using the neural data (spike rates) as inputs for the cognitive models (to drive the accumulators to threshold). A crucial aspect of this procedure is that the models must determine the point in time at which the accumulators start to be driven by the stimulus, because before stimulus onset neural activity is dominated by random noise and is best ignored. For this reason, all models with perfect integration failed, because they were overly impacted by early spiking activity that was unrelated to the stimulus. However, two classes of model were able to account for the behavioral data; leaky integration models effectively attenuate the persistent influence of early noise inputs, and gated integration models block the influence of noise inputs until a certain threshold level of activation has been reached. Once again, behavioral data alone could not distinguish between these competing accounts. However, this model mimicry was resolved by evaluating empirical data collected from movement neurons during the decision making task. Models with leaky integration failed to account for the detailed dynamics in the movement neurons, whereas models with gated integration accounted for these neurophysiological data with impressive precision.

An important remaining challenge is to reconcile the fact that many empirical reports suggest an important, and potentially similar, role for multiple brain regions in perceptual decision making tasks. For example, what is the relationship between integration neurons in the lateral intraparietal (LIP) region, the FEF, and subcortical areas such as the superior colliculus? These areas all exhibit superficial similarities, but neuroanatomical differences – in their connectivity and their respective influence on sensory and motor processes – may play a key role in distinguishing the functional role that each region plays in decision making [40–43].

These case studies highlight ways in which data from neuroscientific experiments might constrain models aimed at characterizing the cognitive architecture of human information processing. This is also a virtue of the cognitive models themselves; the detailed predictions about underlying dynamics that follow from formal cognitive models allow competing accounts to be tested critically given the appropriate constraints – and these constraints may increasingly come in the form of neuroscientific data. The major limitation of this mutually constraining synthesis, and a major challenge for future research, is the need further to validate hypotheses linking neural activity and behavior. 'Linking hypotheses' [12,44] are theories about how the specific, observable aspects of the neuroscientific data should be related to specific, but often latent, aspects of the formal models. For example, are the neural generators that govern behavioral output in a visual two-alternative forced-choice (2AFC) task adequately characterized by single-unit spiking activity in the LIP or FEF? Certainly a great deal of evidence supports this conclusion [21,39], but these conclusions are far from resolved because other areas might contribute to decision processes [45,46]. This lack of resolution highlights the fact that important functional properties may emerge only when neural dynamics are examined across many interconnected brain regions [47,48]. Many important functional characteristics might arise only at the systems level, and such observations will often require a re-evaluation of existing hypotheses linking activity within a specific region and cognition.

Concluding remarks

Model-based cognitive neuroscience is an exciting field that unifies several disciplines that have traditionally operated in relative isolation (Figure 1). We have illustrated how cognitive models can help cognitive neuroscience reach conclusions that are more informative about the cognitive process under study, and we have shown how cognitive neuroscience can help distinguish between cognitive models that provide almost identical predictions for behavioral data.

Within the field of model-based cognitive neuroscience, new trends may evolve in the near future (Box 2). For example, cognitive models are already being extended to account for more detailed aspects of information processing at the level of a single trial [49–51]. As the models become more powerful, the experimental tasks may increase in complexity and ecological validity [26]. In addition, new models may be developed to identify differences in information processing among subsets of participants [52] or subsets of trials [53]. Categorization of different participants and trials may greatly increase the specificity with which neuroscientists draw their conclusions, and the ability of fMRI to examine these differences across large groups of subjects offers an exciting opportunity that complements single-unit recording methods applied to non-human primates.

In summary, the recent focus on combining modeling and cognitive neuroscience holds significant promise for

the field. By fostering this mutually constraining relationship, faster progress will be made, and empirical results will be more firmly grounded in formal theoretical frameworks.

Acknowledgements

This research was supported by VENI and VIDI grants from the Netherlands Organization for Scientific Research (B.U.F. and E.J.W., respectively), Australian Research Council Discovery Project DP0878858 (S.B.), and National Institutes of Mental Health Grant R01-MH092345 (J.T.S.)

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