Chapter 7
Model-Based Cognitive Neuroscience: A Conceptual Introduction

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Abstract This tutorial chapter shows how the separate fields of mathematical psychology and cognitive neuroscience can interact to their mutual benefit. Historically, the field of mathematical psychology is mostly concerned with formal theories of behavior, whereas cognitive neuroscience is mostly concerned with empirical measurements of brain activity. Despite these superficial differences in method, the ultimate goal of both disciplines is the same: to understand the workings of human cognition. In recognition of this common purpose, mathematical psychologists have recently started to apply their models in cognitive neuroscience, and cognitive neuroscientists have borrowed and extended key ideas that originated from mathematical psychology. This chapter consists of three main sections: the first describes the field of mathematical psychology, the second describes the field of cognitive neuroscience, and the third describes their recent combination: model-based cognitive neuroscience.

7.1 Introduction

The griffin is a creature with the body of a lion and the head and wings of an eagle. This mythical hybrid is thought to symbolize the rule over two empires, one on the earth (the lion part) and the other in the skies (the eagle part). The preceding six tutorial chapters may have given the impression that the field of model-based cognitive neuroscience is similar to a griffin in that it represents the union of two fundamentally incompatible disciplines. After all, the methods and concepts from

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Fig. 7.1 The griffin—part lion, part eagle—as depicted in Jonston (1660); copper engraving by Matthius Merian

the field of formal modeling, explained in Chaps. 1, 2, and 3, appear to have little in common with the methods and concepts from the field of cognitive neuroscience as discussed in Chaps. 4, 5, and 6. The goal of this tutorial chapter is to explain that this impression is mistaken—the griffin analogy is apt because it highlights the added possibilities and novel insights that can be obtained when formal models for behavior are combined with methods from cognitive neuroscience ([1; Fig. 7.1).

In this chapter we explain why it is natural to combine behavioral modeling with cognitive neuroscience; furthermore, we illustrate the benefits of the symbiotic relationship between the two disciplines by means of concrete examples. However, before we discuss our model-neuroscience griffin in detail, it is informative to first discuss its component disciplines separately.

7.2 Mathematical Psychology

Mathematical psychologists are concerned with the formal analysis of human behavior. Objects of study include perception, decision-making, learning, memory, attention, categorization, preference judgments, and emotion. Whenever researchers propose, extend, or test formal models of human behavior they are practising mathematical psychology. Thus, the field of mathematical psychology is relatively broad, and defined more by method than by topic or subject matter. To give you an impression of the work done by mathematical psychologists, Table 7.1 provides an overview of the articles published in the June 2012 issue of the *Journal of Mathematical Psychology*.

The inner core of card-carrying mathematical psychologists is comprised of only about a few hundred researchers, and consequently progress in the field can be agonizingly slow. In his 2008 editorial in the *Journal of Mathematical Psychology*, the society's president Jim Townsend wrote:

> It can prove a frustrating experience to compare psychology's pace of advance with progress in the 'hard' sciences. [...] steps in filling in data about a phenomenon not to mention testing of major theoretical issues and models, seem to occur with all the urgency of a glacier. One may wait years, before a modeler picks up the scent of an intriguing theoretical problem and carries it ahead. It is disheartening to contrast our situation with, say, that of microbiology. [9, p. 270]

Table 7.1 Articles published in the June 2012 issue of the *Journal of Mathematical Psychology*

Title	Reference
A tutorial on the Bayesian approach for analyzing structural equation models	[2]
Symmetry axiom of Haken-Kelso-Bunz coordination dynamics revisited in the context of cognitive activity	[3]
Quantum-like generalization of the Bayesian updating scheme for objective and subjective mental uncertainties	[4]
Torgerson's conjecture and Luce's magnitude production representation imply an empirically false property	[5]
A predictive approach to nonparametric inference for adaptive sequential sampling of psychophysical experiments	[6]
On a signal detection approach to m-alternative forced choice with bias, with maximum likelihood and Bayesian approaches to estimation	[7]
How to measure post-error slowing: A confound and a simple solution	[8]

One solution to this glacier-like progress is for mathematical psychologists to collaborate with researchers from other disciplines; when more researchers are interested in a particular phenomenon this greatly increases the speed with which new discoveries are made. This is in fact exactly what happened when cognitive neuroscientists became interested in quantitative models for speeded decision making (e.g., [10–12]; prior to this development, such models were proposed, adjusted, and tested only by a handful of mathematical psychologists—for example, from 1978 to 2001 Roger Ratcliff stood alone in his persistent efforts to promote the *drift diffusion model* as a comprehensive account of human performance in speeded two-choice tasks.

7.2.1 The Drift Diffusion Model

In the drift diffusion model (DDM), shown in Fig. 7.2, noisy information is accumulated over time until a decision threshold is reached and a response is initiated. The DDM provides a formal account of how people make speeded decisions between two choice alternatives. In other words, the model yields parameter estimates (e.g., for drift rate and boundary separation) that represent specific psychological processes (e.g., ability and response caution) in order to account for error rates as well as response time distributions for both correct choices and errors. Put differently, the DDM takes observed behavior—which may be difficult to interpret—and decomposes it into psychological processes that are easier to interpret. For instance, the boundary separation parameter in the DDM reflects the amount of information that a participant seeks to accumulate before being confident enough to respond. Higher levels of boundary separation reflect a more cautious response regime, one in which responding is slow but errors are few.

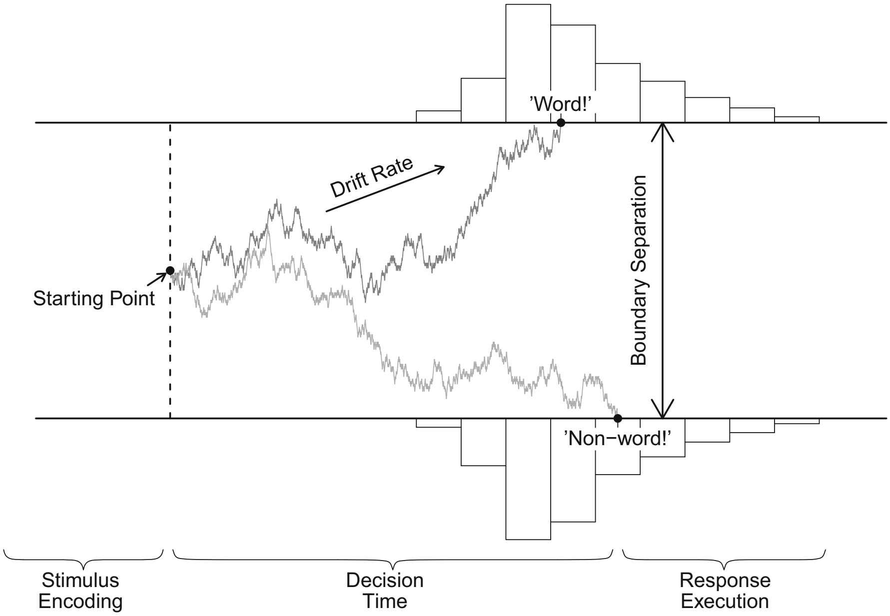

Fig. 7.2 A drift diffusion model for the lexical decision task. In this task, the participant is shown a letter string and has to decide quickly whether it is an existing word (e.g., *tiger*) or not (e.g., *drapa*). Noisy evidence is accumulated over time until a boundary is reached and the corresponding response is initiated. Drift rate quantifies decision difficulty and boundary separation quantifies response caution. Predicted response time equals the decision time plus the time required for non-decision processes such as stimulus encoding and response execution. (Figure as originally published in [13])

Throughout the years, Ratcliff repeatedly demonstrated how the DDM allows for deeper insight in the processes that underlie observed behavior (e.g., [14]). Consider, for instance, the finding that older adults respond more slowly than younger adults, a general empirical regularity that holds even in relatively simple tasks such as lexical decision. The once-dominant explanation of this age-related slowing holds that older adults have a reduced rate of information processing, perhaps as a result of neural degradation; hence, the age-related slowing was assumed to hold generally, across a wide range of different tasks and processes [15–17]. However, when the DDM was applied to the data from older adults, Ratcliff and colleagues discovered something surprising [18, 19]: in most speeded two-choice tasks, drift rates did *not* differ between the young and the old. That is, older adults were accumulating diagnostic information as efficiently as the young. Instead, the age-related slowdown was usually due to a combination of two factors: (1) an increase in non-decision time, that is, the time needed for encoding and response execution, and (2) an increase in response caution. These results suggest that the age-related slowing can be undone, at least in part, by encouraging the elderly to adopt a more risky response strategy (for a confirmation of this prediction see for instance [20]).

Currently, the DDM can be considered one of the most successful quantitative models in mathematical psychology: not only does it provide fits to empirical data that are consistently good, it has also driven theoretical progress in fields traditionally dominated by verbal or quasi-formal accounts. These intuitive accounts were often unable to withstand quantitative scrutiny (e.g., [21]).

The main weakness of the DDM is that it provides a decomposition of performance that is relatively abstract, that is, the DDM does not commit to any representational assumptions. This makes the model less interesting from a psychological point of view. The main weakness of the DDM, however, is also its main strength: because its account is relatively abstract it can be applied to a wide range of different tasks and paradigms.

For the first 25 years, the development and application of the DDM was guided by statistical and pragmatic considerations; Of particular relevance here is that the dynamics of decision-making in neural circuits is remarkably similar to that postulated by the DDM (e.g., [12]) in that neurons appear to accumulate noisy evidence until threshold. Thus, the DDM does not only capture behavioral data but holds the promise to capture underlying neural dynamics as well. This may not be accidental: the DDM describes performance of a decision-maker who is statistically optimal in the sense of minimizing mean response time for a fixed level of accuracy (e.g., [22]) and it is plausible that for simple perceptual tasks, evolution and individual learning has curtailed those neural dynamics that lead to suboptimal outcomes. Cognitive neuroscientists have not only applied the DDM to neural data, they have also proposed theoretical extensions to the model. For instance, high-profile extensions concern the generalization to more than two choice-alternatives [23, 24], collapsing bounds [25], urgency-gating [26], and drift rates that change during stimulus processing [27].

7.2.2 Ambivalence Towards Neuroscience

Although mathematical psychologists are increasingly interested in the neural underpinnings of cognition, the overall attitude towards the neurosciences is one of ambivalence or even open distrust.[1] Some of this ambivalence stems from the concern that brain measurements alone may not be theoretically meaningful. For instance, Coltheart claimed that "no functional neuroimaging research to date has yielded data that can be used to distinguish between competing psychological theories" [28, p. 323] (see the exercise at the end of this chapter).

To demonstrate the limitations of neuroscientific methods, Ulrich presented the following thought experiment [29]. Suppose you are intrigued by the ability of a computer program to provide analytic solutions to integrals. In the Maple program, for instance, you can enter the integral $\int x \sin x \, \mathrm{d}x$ as `int(x*sin(x),x);` and Maple will immediately return the solution: `sin(x)-x*cos(x)`. How can we learn more about how Maple accomplishes these and other computations?

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[1] At the 2009 annual meeting of the *Society for Mathematical Psychology*, one of the plenary speakers discussed some of his beginning exploits in cognitive neuroscience. Following his talk, the first question from the audience was whether he had now "joined the dark force".

Ulrich argues that neuroscientists may tackle this problem in different ways, as illustrated in Fig. 7.3: analogous to functional brain imaging, one might perform a heat scan on the laptop as it computes integrals, and compare this with a control condition where it is just waiting for input (Fig. 7.3, top left panel). Analogous to EEG measurements, one could attach surface electrodes to the laptop, have the laptop repeatedly perform integrals, and compute a stimulus-locked or a response-locked event-related potential (Fig. 7.3, top right panel). Analogous to single-cell recordings in monkeys, one might implant electrodes and register the activity of small components within the laptop (Fig. 7.3, lower left panel). Finally, analogous to neurosurgical methods, one might lesion the laptop, for instance by hitting it with a hammer. With luck, one might even discover a double dissociation, that is, lesioning one part of the laptop harms the computation of integrals but does not harm word processing, whereas lesioning another part of the laptop harms word processing but not the computation of integrals (Fig. 7.3, lower right panel).

Ulrich ([29, p. 29]) concludes that "(...) none of these fancy neuroscience techniques can directly unravel the hidden mechanisms of this symbolic math program" and hence, brain measurement techniques alone cannot replace formal theories of cognition. We suspect that most mathematical psychologists subscribe to the Ulrich laptop metaphor of neuroscience. The laptop metaphor is insightful and thought-provoking, but it should not be misinterpreted to mean that neuroscientific methods are by definition uninformative. For example, consider a race of aliens who discover a refrigerator and wish to learn how it works. They may first conduct behavioral experiments and conclude that parts of the refrigerator are cooler then others. They may study the speed of cooling in the different compartments, and its relation to a host of relevant factors (e.g., the extent to which the refrigerator door is left open, the temperature of various products just before they are put inside, and the volume occupied by the products). The aliens may develop theoretical concepts such as homeostasis, they may propose sets of axioms, and they may develop competing formal models about how the refrigerator does what it does. Unfortunately, the behavioral data are rather sparse and therefore they will fail to falsify many of the more complicated theories. It is evident that "neuroscientific" measures of studying the refrigerator (e.g., examining its underlying circuitry) will yield additional insights that can be used either to adjudicate between the competing theories or to develop new theories that are more appropriate.

We will leave it up to philosophers to decide whether the study of cognition is similar to a laptop or to a refrigerator. This decision may well depend on the cognitive phenomenon under study. For instance, perceptual illusions are perhaps best understood by taking into account the neural processes that subserve perception, whereas a different approach is warranted when one wants to understand loss-aversion in gambling.

Pragmatically, any approach is worthwhile as long as it yields theoretical progress, that is, a deeper understanding of human cognition. It is undeniably true that brain measurements, just as response times or error rates, constitute data that are potentially informative about the underlying cognitive process. The main difficulty, therefore, is to develop formal models that allow the brain measurements to make contact with putative cognitive processes.

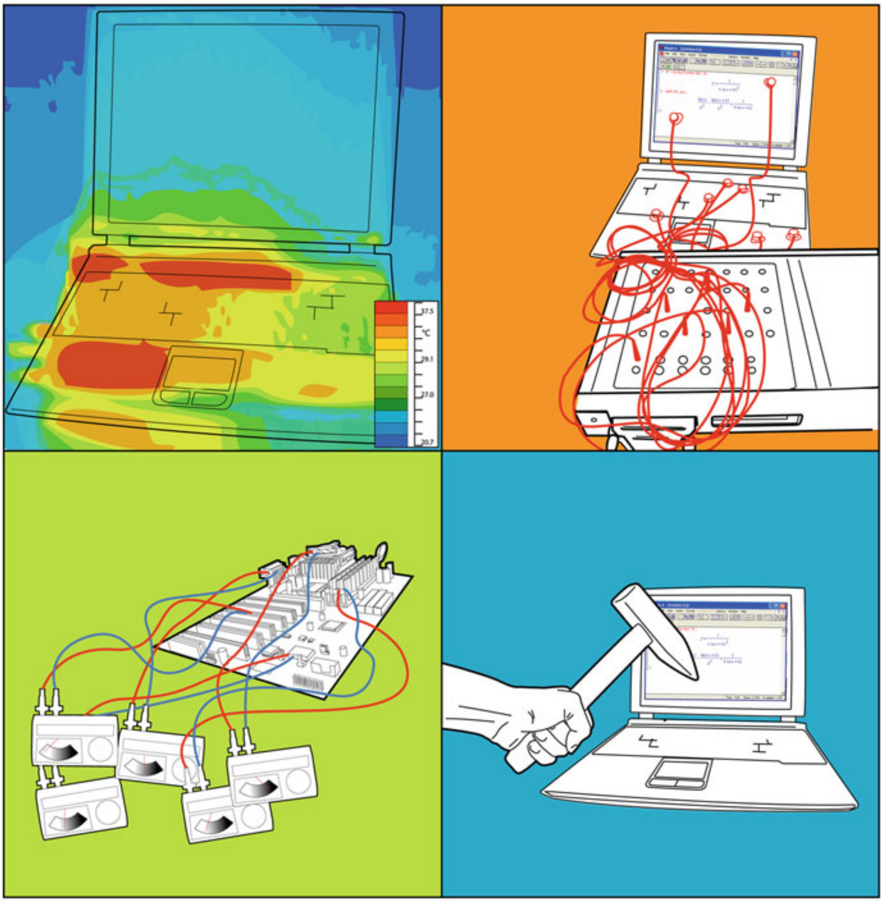

Fig. 7.3 Illustration of Ulrich's thought experiment. The operations of a computer program are studied with methods from neuroscience. *Top left panel*: heat radiation scan; *top right panel*: event-related potentials; *lower left panel*: single-unit recordings; *lower right panel*: experimental lesions. Figure reprinted with permission from [29]

7.3 Cognitive Neuroscience

The annual meetings of the *Society for Neuroscience* attract up to 40,000 participants, and plenary lectures are given by celebrities such as the Dalai Lama. Based on the attendance to their respective annual meeting, neuroscientists outnumber mathematical psychologist by a factor of 200 to 1. Cognitive neuroscientists use brain measurement techniques to study cognitive processes such as perception, attention, learning, emotion, decision-making, etc. Most of this work involves an empirical comparison between groups, treatments, or experimental conditions. For instance, Rouw and Scholte [30] compared a group of control participants with a group of

Table 7.2 First seven articles published in the June 2012 issue of the *Journal of Cognitive Neuroscience*

Title	Reference
Focal brain lesions to critical locations cause widespread disruption of the modular organization of the brain	[33]
Playing a first-person shooter video game induces neuroplastic change	[34]
Closing the gates to consciousness: Distractors activate a central inhibition process	[35]
TMS of the FEF interferes with spatial conflict	[36]
Local field potential activity associated with temporal expectations in the macaque lateral intraparietal area	[37]
Spatio-temporal brain dynamics mediating post-error behavioral adjustments	[38]
Hippocampal involvement in processing of indistinct visual motion stimuli	[39]

grapheme-color synesthetes, people who experience a specific color whenever they see a particular letter or number (e.g., “T is bright red”). Diffusion tensor imaging confirmed the hypothesis that the added sensations in synesthesia are associated with more coherent white matter tracts in various brain areas in frontal, parietal, and temporal cortex. In another example, Jepma and Nieuwenhuis [31] used a reinforcement learning task in which participants have to maximize rewards by making a series of choices with an uncertain outcome. The main result was that baseline pupil diameter was larger preceding exploratory choices (i.e., choices associated with a large uncertainty in outcome) than it was preceding exploitative choices (i.e., choices associated with a small uncertainty in outcome). Pupil diameter is an indirect marker for the activity of the locus coeruleus, a nucleus that modulates the norepinephrine system. Hence, the results are consistent with *adaptive gain theory*, according to which activity in the locus coeruleus regulates the balance between exploration and exploitation. A final example concerns the work by Ding and Gold [32], who showed that electrical microstimulation of the monkey caudate nucleus biases performance in a random-dot motion task.[2] This result suggests that the caudate has a causal role in perceptual decision making.

To give you a further impression of the work done by cognitive neuroscientists, Table 7.2 provides an overview of the articles published in the June 2012 issue of the *Journal of Cognitive Neuroscience*. Compared to the mathematical psychology approach, the cognitive neuroscience approach is geared towards understanding cognition on a relatively concrete level of implementation: what brain areas, neural processes, and circuits are involved in a particular cognitive process?

It is tempting to believe that the level of implementation is the level that is somehow appropriate for the study of cognition. This is suggested, for example, by the adage “the mind is what the brain does”. However, Ulrich’s laptop metaphor shows that such a conclusion is premature; clearly, the analytical integration that Maple

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[2] In this popular perceptual task, the participant has to judge the apparent direction of a cloud of moving dots.

accomplishes is "what the laptop does", but it does not follow that we need or want to study the properties of the laptop in order to understand how Maple handles integrals analytically. Thus, even though "the mind is what the brain does", it is not automatically the case that when we measure the brain we learn a great deal about the mind. Readers who doubt this statement are advised to read the contributions that follow the article by Coltheart [28]; here, the discussants have to put in hard work to come up with just a single example of how functional neuroimaging has provided data to discriminate between competing psychological theories.

In order for cognitive neuroscience to have impact on psychological theory, it is important that the two are linked [40–42]. One way to accomplish such linking is by elaborating the psychological theory such that it becomes explicit about the brain processes involved [43]; another way is by using formal models to connect findings from neuroscience to the cognitive processes at hand. For instance, a mathematical psychologist may use the DDM to state that, when prompted to respond quickly, participants become less cautious, that is, they require less evidence before they are willing to make a decision. This description of cognition is relatively abstract and does not speak to how the brain implements the process. A neuroscientist may make this more concrete and suggest that the instruction to respond quickly leads to an increase of the baseline level of activation in the striatum, such that less input from cortex is needed to suppress the output nuclei of the basal ganglia, thereby releasing the brain from tonic inhibition and allowing an action to be executed [44, 45]. Thus, the DDM may provide an estimate of a latent cognitive process (e.g., response caution) which may then be compared against activation patterns in the brain. By using formal models that estimate psychological processes, this particular neuroscience approach furthers real theoretical progress and potentially bridges the divide between the implementational level and the algorithmic level [46].

7.4 Model-Based Cognitive Neuroscience: Symbiosis of Disciplines

The goal of model-based cognitive neuroscience is to bridge the gap between brain measurements and cognitive process with the help of formal models (e.g.,[10, 47–51]). This interdisciplinary approach is illustrated in Fig. 7.4. The figure shows that experimental psychology, mathematical psychology, and cognitive neuroscience all pursue a common goal: a better understanding of human cognition. It is often difficult, however, to learn about the relevant cognitive processes from the data directly – often, one first needs a mathematical model to provide quantitative estimates for the cognitive processes involved. Next, the estimates of the cognitive processes can be related to the brain measurements.

The "model-in-the-middle" [52] symbiosis of disciplines is useful in several ways. Rather than discuss the advantages abstractly, the next two sections provide concrete illustrations of the mutually beneficial relationship between mathematical models and brain measurements (see also [1]).

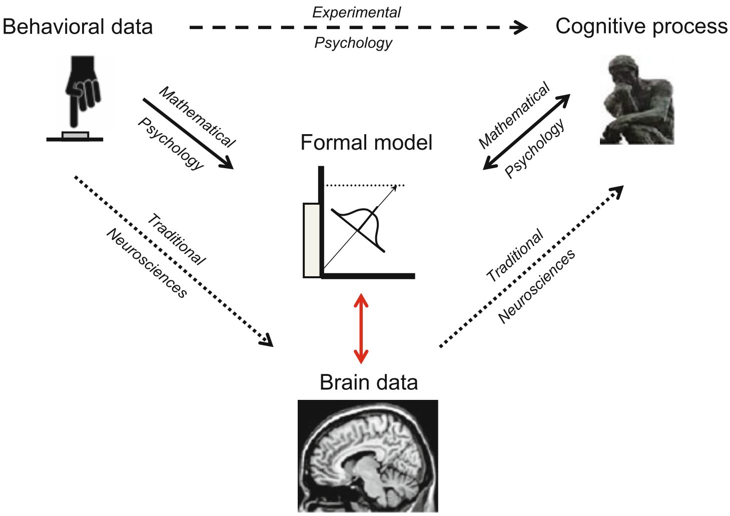

Fig. 7.4 The model-in-the-middle approach unites experimental psychology, mathematical psychology, and cognitive neuroscience, as the main goal of all three disciplines is to understand more deeply the processes and mechanisms that constitute human cognition. The *red* arrow indicates the reciprocal relation between measuring the brain and modeling behavioral data. (Figure reprinted with permission from [1])

7.4.1 Use of Mathematical Models for Cognitive Neuroscience

Mathematical models are useful in many ways. First, they decompose observed behavioral data into latent cognitive processes. Brain measurements can then be associated with particular cognitive processes instead of behavioral data. For example, Chap. 2 explained how the LBA model—just as the DDM model discussed in Sect. 7.2 and in Chap. 3—decomposes response time distributions and error rates into underlying concepts such as *response caution* and the *speed of information processing*. This decomposition can be used to demonstrate that a particular experimental manipulation had the desired effect. For instance, participants in a study by Forstmann and colleagues [44] performed a random-dot motion task under various cue-induced levels of speed-stress. That is, before each stimulus a cue indicated whether the stimulus needed to be classified accurately or quickly. Because the authors were interested in the neural basis of the speed-accuracy tradeoff, they hoped that the cue would selectively affect the LBA response caution parameter. And indeed, the model decomposition confirmed that this was the case. Note that without concrete model fitting, this conclusion had been premature, unwarranted, and potentially misleading—it is certainly possible that instructions to respond more quickly can, for some tasks, also induce a change in speed of processing, or a change in the time required for peripheral processes.

Another advantage that the model-based decomposition brings is that, even when a particular manipulation is not process-pure, one may associate brain measurements specifically with the parameter of interest. For instance, suppose that in the speed-accuracy experiment by Forstmann and colleagues [44], a cue to respond more quickly had also lowered the speed of information processing. This means that the critical fMRI contrasts are contaminated because they reflect a combination of two effects: the change in response caution associated with the speed-accuracy tradeoff, and the change in drift rate associated with the lower speed of processing. One method to address this complication is to correlate the contaminated brain measures (e.g., the average change in the BOLD response for each participant) with the process of interest (e.g., the individual estimates of the change in response caution), perhaps after partialling out the effects of the nuisance process. This method identifies those voxels that relate to the cognitive construct of response caution.

Finally, the model-based decomposition allows one to take into account individual differences. For instance, Forstmann and colleagues [44] found that speed cues activated the right anterior striatum and the right pre-supplementary motor area (pre-SMA). This result was corroborated by an analysis of individual differences: participants with a relatively large cue-induced decrease in response caution also showed a relatively large increase in activation in the right anterior striatum and right pre-SMA. Of course, such an analysis is only meaningful if there are substantial individual differences to begin with; if all participants respond to the cue in approximately the same way then the group-average result will be highly significant but the individual difference analysis may not be significant at all.

In another example of the importance of individual differences, Forstmann and colleagues [53] studied the neural basis of prior knowledge in perceptual decision-making. As before, participant performed a random-dot motion task; this time, the cue gave prior information about the likely direction of movement of the upcoming stimulus. The cue “L9”, for example, indicated that the probability was 90 % that the upcoming stimulus would move to the left (see also [54]). The cue-induced bias was clearly visible in the behavioral data: responses were much faster and more often correct when the cue was reliable and informative. Surprisingly, however, the fMRI contrast did not reveal any significant results. After including an LBA response bias parameter as a covariate in the fMRI analysis, however, the results showed significant cue-related activation in regions that generally matched the theoretical predictions (e.g., putamen and orbitofrontal cortex). The reason for the discrepancy is that by adding the response bias parameter we can account for individual differences in people’s reactions to the cue. Some participants exhibited a lot of bias, and others only a little. These individual differences in the latent cognitive process are usually not incorporated the fMRI analysis and hence add to the error term instead. By explicitly accounting for individual differences the error term is reduced and experimental power is increased.

Mathematical models are also useful because they can drive the search for brain areas involved in a particular cognitive function. In fMRI research, for instance, this means that a model’s predictions are convolved with the hemodynamic response function. Next, the predicted blood oxygenation level dependent signal (BOLD) response profiles are used to search for areas in the brain with similar activation profiles. The search can be exploratory or more confirmatory. A prominent example of the latter approach is the recent work that attempts to link the components of the ACT-R model to different brain regions (see the final chapter of this book as well as [55, 56]).

Another way in which mathematical models are useful is that they may help demonstrate that performance in superficially different tasks may be driven by the same cognitive process. For example, the cognitive neuroscience literature suggests that perceptual categorization and old-new recognition are subserved by separate neural systems. In contrast, mathematical models of these tasks suggests that similar processes are involved. Specifically, exemplar models posit that people categorize a test object by comparing it to exemplars stored in memory. Both categorization and recognition decisions are thought to be based on the summed similarity of the test object to the exemplars [57, 58]. These conflicting perspectives were recently reconciled by Nosofsky and colleagues [59], who argued that categorization and recognition differ not in terms of the underlying process, but in terms of the underlying criterion settings: in recognition, the criterion needs to be strict, since the test object needs to match one of the study items exactly; in categorization, the criterion can be more lax, as exact matches are not needed. In an fMRI experiment, Nosofsky and colleagues [59] induced participants to use different criterion settings; the resulting data were then fit by an exemplar model. Results confirmed that (1) the exemplar model provides a good account of both categorization and recognition, with only criterion settings free to vary; (2) the average task-related differences in brain activation can be explained by differences in evidence accumulation caused by systematically varying criterion settings; and (3) participants with high criterion settings show large BOLD differences between old and random stimuli in the frontal eye fields and the anterior insular cortex. Hence, Nosofsky and colleagues [59] concluded that there is little evidence that categorization and recognition are subserved by separate memory systems. The most important lesson to be learned from this work is that differences in brain activation do not necessarily indicate different underlying mechanisms or processes. Differences in brain activation can also come about through differences in stimulus surface features (which Nosofsky et al. controlled for) and differences in criterion settings. A mathematical model can estimate these criterion settings and allow a statistical assessment of their importance.

In addition to the above, mathematical models have general worth because they provide (1) a concrete implementation of a theoretical framework; (2) a coherent interpretive framework; and (3) a guide to experimental manipulations that are particularly informative. In sum, it is evident that for cognitive neuroscience, the use of mathematical models comes with considerable advantages. The reverse—the advantages of cognitive neuroscience for mathematical models—is the topic of the next section.

7.4.2 *Use of Cognitive Neuroscience for Mathematical Models*

Until recently, findings from cognitive neuroscience had little impact on model development in mathematical psychology. Exceptions that confirm the rule are parallel distributed processing models [60, 61] and neurocomputational models developed to take into account the details of neural processing [43, 62–64]. This state of affairs is changing, and for good reason: response times, error rates, and confidence judgements ultimately provide little information to tell apart mathematical models with incompatible assumptions and architectures [41]. For instance, Ditterich [23] showed that behavioral data are insufficient to discriminate between multiple-choice response time models that have evidence integrators with and without leakage, with and without feedforward and feedback inhibition, and with and without linear and non-linear mechanisms for combining information across choice alternatives. Neural data, however, can able to adjudicate between the hypothesized mechanisms, at least in potentia [23].

As a specific example, consider a generic response time model with N evidence accumulators, one for each choice alternative, that race to a threshold. The model can account for the speed-accuracy tradeoff by changing the distance from baseline to threshold. However, the model is mute on whether instructions to respond accurately increase threshold or decrease baseline; in fact, these mechanisms are mathematically equivalent. Nevertheless, the mechanisms are not conceptually equivalent, and neural data could discriminate between the two accounts. A similar example considers the change in processing that occurs as the number of incorrect choice alternatives increases. Such an increase in task difficulty requires a longer period of evidence accumulation in order to reach an acceptable level of accuracy in identifying the target alternative. The evidence accumulation process can be extended either by increasing thresholds or by decreasing the baseline. Using behavioral data, there is no way to tell these two mechanisms apart. However, Churchland and colleagues [65] used single-cell recordings to show that, confronted with the prospect of having to chose between four instead of two random-dot choice alternatives, monkeys had decreased firing rates in the lateral intraparietal area. These single cell recordings are consistent with a changing baseline account rather than a shifting threshold account.

Hence, the general promise is that data from cognitive neuroscience may provide additional constraints. An interesting illustration of this principle is provided by Purcell and colleagues [66], who studied how monkeys perform a visual search task in which they have to make an eye movement toward a single target presented among seven distractors. Several models were fit to the data, and initial constraint was gained by using the measured spike trains as input to the evidence accumulators. This creates an immediate challenge: the models must determine when the accumulators start to be driven by the stimulus, because the neural activity that precedes stimulus onset is uninformative and its accumulation can only harm performance. Hence, models with perfect integration failed, as they were overly impacted by early spiking activity that was unrelated to the stimulus. Models with leaky integration did not suffer from early spiking activity, but their predictions were inconsistent with another neural constraint: the spiking activity from movement neurons. In the end, the only class of models that survived the test were gated integration models, models that block the influence of noise inputs until a certain threshold level of activation is reached.

In general, it is clear that neuroscience data hold tremendous potential for answering questions that mathematical psychologists can never address with behavioral data alone.

7.5 Open Challenges

The above examples have only scratched the surface of the work conducted within model-based cognitive neuroscience. Nevertheless, the field can greatly expand by considering a broader range of mathematical models, and a broader range of brain measures (e.g., structural MRI, event-related potentials in EEG, genetics, pharmacology, etc.). Also, model dynamics can be linked more closely to brain dynamics, either by constructing a single overarching statistical model, or by developing single trial estimates of cognitive processes. For example, van Maanen and colleagues [67] extended the LBA model to estimate drift rate and thresholds on a trial-by-trial basis. This allows a more direct comparison with neurophysiological data, which also vary on a trial-by-trial basis.

Another challenge is to balance the desire for parsimonious models (i.e., models with few parameters and clear mechanisms) against the reality of the brain's overwhelming complexity. The appropriate level of model complexity depends very much on the goals of the researchers. If the goal is to obtain estimates of latent cognitive processes, then the model needs to be relatively simple—the behavioral data simply do not provide sufficient support for models that are relatively complex. On the other hand, if the goal is to create a model that accounts for the detailed interactions between neurons or brain systems, the model needs to be more intricate.

A final challenge is that, despite the intuitive attractiveness of results from rats and monkeys, we should remain aware of the possibility that some of the results obtained with these species may not carry over to humans. This may be due to differences in anatomy, but other factors can contribute as well. For instance, recent work suggests that monkeys who perform a speeded choice task may experience an increased urgency to respond [26] that can expresses itself in response thresholds that decreases over time [25, 68]. Before concluding that response urgency or collapsing bounds are a universal signature of human decision making, however, we need to make sure that the pattern in monkeys is obtained in humans as well. This requires a careful modeling exercise in which benchmark data sets are fit with two versions of the same sequential sampling model: one that has constant thresholds and one that has collapsing bounds [69]. It is entirely possible, for instance, that collapsing bounds are used by monkeys because they want to maximize reward rate [68]; first-year psychology undergraduates, however, are usually not reinforced with squirts of orange juice and may approach the task with a different goal. The collapsing-bound hypothesis shows promise and is worth exploring, but its generality is pending investigation.

7.6 Concluding Comments

The examples in this chapter have shown how mathematical models can advance cognitive neuroscience, and how cognitive neuroscience can provide constraint for mathematical models. The increasing collaboration between these historically separate fields of study is an exciting new development that we believe will continue in the future.

Exercises

1. Section 7.2: in what sense is the DDM similar to signal-detection theory?
2. Section 7.2: Can you find a concrete example to refute Coltheard's claim that "no functional neuroimaging research to date has yielded data that can be used to distinguish between competing psychological theories"?
3. Section 7.3: Read the articles by Miller [70] and by Insel [71] on the impact of neuroscience on psychiatry and clinical psychology. Who do you agree with, and why?
4. Section 7.2: Read the Gold and Shadlen [12] article and prepare a 30-min presentation on it, critically summarizing and explaining its content.
5. Describe a mathematical model (not discussed in this chapter) that could find application in cognitive neuroscience.
6. Mention one pro and one con for each of the following brain measures: single-cell recordings, ERP, fMRI, and DWI.
7. Can you think of concrete research questions in cognitive neuroscience that could profit from a model-based approach?

Further Reading

1. Ratcliff and McKoon [74] offer an overview of the drift diffusion model and its relation to cognitive neuroscience.
2. http://neuroskeptic.blogspot.com/2012/02/mystery-joker-parodies-neuroscience.html tells a tale about neuroscience and Sigmund Freud.
3. Churchland and Ditterich [75] discuss recent developments in models for a choice between multiple alternatives.
4. We consider our work on bias [53] as one of our better efforts. Unfortunately, the reviewers did not agree, and one even commented "Flawed design, faulty logic, and limited scholarship engender no confidence or enthusiasm whatsoever".

References

1. Forstmann BU, Wagenmakers EJ, Eichele T, Brown S, Serences JT (2011) Reciprocal relations between cognitive neuroscience and formal cognitive models: Opposites attract? Trends Cognit Sci 15:272
2. Song XY, Lee SY (2012) A tutorial on the Bayesian approach for analyzing structural equation models. J Math Psychol 56:135
3. Frank TD, Silva PL, Turvey MT (2012) Symmetry axiom of Haken–Kelso–Bunz coordination dynamics revisited in the context of cognitive activity. J Math Psychol 56:149
4. Asano M, Basieva I, Khrennikov A, Ohya M, Tanaka Y (2012) Quantum-like generalization of the Bayesian updating scheme for objective and subjective mental uncertainties. J Math Psychol 56:166
5. Luce RD (2012) Torgerson's conjecture and Luce's magnitude production representation imply an empirically false property. J Math Psychol 56:176
6. Poppe S, Benner P, Elze T (2012) A predictive approach to nonparametric inference for adaptive sequential sampling of psychophysical experiments. J Math Psychol 56:179
7. DeCarlo LT (2012) On a signal detection approach to m–alternative forced choice with bias, with maximum likelihood and Bayesian approaches to estimation. J Math Psychol 56:196
8. Dutilh G van Ravenzwaaij D, Nieuwenhuis S, van der Maas HLJ, Forstmann BU, Wagenmakers EJ (2012) How to measure post–error slowing: A confound and a simple solution. J Math Psychol 56:208
9. Townsend JT (2008) Mathematical psychology: Prospects for the 21st century: A guest editorial. J Math Psychol 52:269
10. Gold JI, Shadlen MN (2001) Neural computations that underlie decisions about sensory stimuli. Trends Cognit Sci 5:10
11. Gold JI, Shadlen MN (2002) Banburismus and the brain: Decoding the relationship between sensory stimuli, decisions, and reward. Neuron 36:299
12. Gold JI, Shadlen MN (2007) The neural basis of decision making. Annu Rev Neurosci 30:535
13. van Ravenzwaaij D, Mulder M, Tuerlinckx F, Wagenmakers EJ (2012) Do the dynamics of prior information depend on task context? An analysis of optimal performance and an empirical test. Front Cognit Sci 3:132
14. Wagenmakers EJ (2009) Methodological and empirical developments for the Ratcliff diffusion model of response times and accuracy. Eur J Cognit Psychol 21:641
15. Brinley JF (1965) Cognitive sets, speed and accuracy of performance in the elderly. In: Welford AT, Birren JE (eds) Behavior, aging and the nervous system. Thomas, Springfield, pp 114–149
16. Cerella J (1985) Information processing rates in the elderly. Psychol Bull 98:67
17. Salthouse TA (1996) The processing–speed theory of adult age differences in cognition. Psychol Rev 103:403
18. Ratcliff R, Thapar A, Gomez P, McKoon G (2004) A diffusion model analysis of the effects of aging in the lexical–decision task. Psychol Aging 19:278
19. Ratcliff R, Thapar A, McKoon G (2007) Application of the diffusion model to two–choice tasks for adults 75–90 years old. Psychol Aging 22:56
20. Ratcliff R, Thapar A, McKoon G (2004) A diffusion model analysis of the effects of aging on recognition memory. J Mem Lang 50:408
21. Wagenmakers EJ, Ratcliff R, Gomez P, McKoon G (2008) A diffusion model account of criterion shifts in the lexical decision task. J Mem Lang 58:140
22. Bogacz R, Brown E, Moehlis J, Holmes P, Cohen JD (2006) The physics of optimal decision making: A formal analysis of models of performance in two-alternative forced choice tasks. Psychol Rev 113:700
23. Ditterich J (2010) A comparison between mechanisms of multi–alternative perceptual decision making: Ability to explain human behavior, predictions for neurophysiology, and relationship with decision theory. Front Decis Neurosci 4:184
24. Usher M, McClelland JL (2001) On the time course of perceptual choice: The leaky competing accumulator model. Psychol Rev 108:550

25. Drugowitsch J, Moreno–Bote R, Churchland AK, Shadlen MN, Pouget A (2012) The cost of accumulating evidence in perceptual decision making. J Neurosci 32:3612
26. Cisek P, Puskas GA, El–Murr S (2009) Decisions in changing conditions: The urgency–gating model. J Neurosci 29:11560
27. Krajbich I, Armel C, Rangel A (2010) Visual fixations and comparison of value in simple choice. Nat Neurosci 13:1292
28. Coltheart M (2006) What has functional neuroimaging told us about the mind (so far)? Cortex 42:323
29. Ulrich R (2009) Uncovering unobservable cognitive mechanisms: The contribution of mathematical models. In: Rösler F, Ranganath C, Röder B, Kluwe RH (eds) Neuroimaging of human memory: linking cognitive processes to neural systems. Oxford University Press, Oxford, pp 25–41
30. Rouw R, Scholte HS (2007) Increased structural connectivity in grapheme-color synesthesia. Nat Neurosci 10:792
31. Jepma M, Nieuwenhuis S (2011) Pupil diameter predicts changes in the exploration-exploitation trade-off: Evidence for the adaptive gain theory. J Cognit Neurosci 23:1587
32. Ding L, Gold JI (2012) Separate, causal roles of the caudate in saccadic choice and execution in a perceptual decision task. Neuron 75:865
33. Gratton C, Nomura EM, Pérez F, D'Esposito M (2012) Focal brain lesions to critical locations cause widespread disruption of the modular organization of the brain. J Cognit Neurosci 24:1275
34. Wu S, Cheng CK, Feng J, D'Angelo L, Alain C, Spence I (2012) Playing a first–person shooter video game induces neuroplastic change. J Cognit Neurosci 24:1286
35. Niedeggen M, Michael L, Hesselmann G (2012) Closing the gates to consciousness: Distractors activate a central inhibition process. J Cognit Neurosci 24:1294
36. Bardi L, Kanai R, Mapelli D, Walsh V (2012) TMS of the FEF interferes with spatial conflict. J Cognit Neurosci 24: 1305
37. Premereur E, Vanduffel W, Janssen P (2012) Local field potential activity associated with temporal expectations in the macaque lateral intraparietal area. J Cognit Neurosci 24:1314
38. Manuel AL, Bernasconi F, Murray MM, Spierer L (2012) Spatio–temporal brain dynamics mediating post–error behavioral adjustments. J Cognit Neurosci 24:1331
39. Fraedrich EM, Flanagin VL, Duann JR, Brandt T, Glasauer S (2012) newblock Hippocampal involvement in processing of indistinct visual motion stimuli. JJ Cognit Neurosci 24:1344
40. Brown SD (2012) Common ground for behavioural and neuroimaging research. Aust J Psychol 64:4
41. Schall JD (2004) On building a bridge between brain and behavior. Annu Rev Psychol 55:23
42. Teller D (1984) Linking propositions. Vis Res 24:1233
43. Ashby FG, Helie S (2011) A tutorial on computational cognitive neuroscience: Modeling the neurodynamics of cognition. J Math Psychol 55:273
44. Forstmann BU, Dutilh G, Brown S, Neumann J, von Cramon DY, Ridderinkhof KR, Wagenmakers EJ (2008) Striatum and pre–SMA facilitate decision–making under time pressure. Proc Natl Acad Sci U S A 105:17538
45. Mink JW (1996) The basal ganglia: Focused selection and inhibition of competing motor programs. Prog Neurobiol 50:381
46. Marr D (1982) Vision: a computational investigation into the human representation and processing of visual information. Henry Holt and Company, San Francisco (H W. Freeman)
47. Dolan RJ (2008) Neuroimaging of cognition: Past, present, and future. Neuron 60:496
48. Friston KJ (2009) Modalities, modes, and models in functional neuroimaging. Science 326:399
49. Hanes DP, Schall JD (1996) Neural control of voluntary movement initiation. Science 274:427
50. Mars RB, Shea NJ, Kolling N, Rushworth MF. (2012) Model-based analyses: Promises, pitfalls, and example applications to the study of cognitive control. Q J Exp Psychol (Hove), 65(2): 252–67
51. O'Doherty JP, Hampton A, Kim H (2007) Model–based fMRI and its application to reward learning and decision making. Ann N Y Acad Sci 1104:35

52. Corrado G, Doya K (2007) Understanding neural coding through the model–based analysis of decision making. J Neurosci 27:8178
53. Forstmann BU, Brown S, Dutilh G, Neumann J, Wagenmakers EJ (2010) The neural substrate of prior information in perceptual decision making: A model-based analysis. Front Hum Neurosci 4:40
54. Mulder M, Wagenmakers EJ, Ratcliff R, Boekel W, Forstmann BU (2012) Bias in the brain: A diffusion model analysis of prior probability and potential payoff. J Neurosci 32:2335
55. Anderson JR, Fincham JM, Qin Y, Stocco A (2008) A central circuit of the mind. Trends Cognit Sci 12:136
56. Borst JP, Taatgen NA, Stocco A van Rijn H (2010) The neural correlates of problem states: Testing fMRI predictions of a computational model of multitasking. PLoS ONE 5
57. Nosofsky RM (1986) Attention, similarity, and the identification–categorization relationship. J Exp Psychol: Gener 115:39
58. Nosofsky RM, Palmeri TJ (1997) An exemplar–based random walk model of speeded classification. Psychol Rev 104:266
59. Nosofsky RM, Little DR, James TW (2012) Activation in the neural network responsible for categorization and recognition reflects parameter changes. Proc Natl Acad Sci U S A 109:333
60. Rumelhart DE, Hinton GE, McClelland JL (1986) A general framework for parallel distributed processing. In: Rumelhart DE, McClelland JL, the PDP Research Group (eds) Parallel distributed processing: explorations in the microstructure of cognition (Vol 1). MIT Press, Cambridge, pp. 45–76
61. Rumelhart DE, Hinton GE, Williams RJ (1986) Learning internal representations by error propagation. In: Rumelhart DE, McClelland JL, the PDP Research Group (eds) Parallel distributed processing: explorations in the microstructure of cognition, Vol 1. MIT Press, Cambridge, pp 318–362
62. Ratcliff R, Frank MJ (2012) Reinforcement–based decision making in corticostriatal circuits: Mutual constraints by neurocomputational and diffusion models. Neural Comput 24:1186
63. Stocco A, Lebiere C, Anderson JR (2010) Conditional routing of information to the cortex: A model of the basal ganglia's role in cognitive coordination. Psychol Rev 117:541
64. Stocco A (2012) Acetylcholine–based entropy in response selection: A model of how striatal interneurons modulate exploration, exploitation, and response variability in decision–making. Front Neurosci 6:18
65. Churchland AK, Kiani R, Shadlen MN (2008) Decision–making with multiple alternatives. Nat Neurosci 11:693
66. Purcell BA, Heitz RP, Cohen JY, Schall JD, Logan GD, Palmeri TJ (2010) Neurally constrained modeling of perceptual decision making. Psychol Rev 117:1113
67. van Maanen L, Brown S, Eichele T, Wagenmakers EJ, Ho T, Serences J, Forstmann BU (2011) Neural correlates of trial–to–trial fluctuations in response caution. J Neurosci 31:17488
68. Deneve S (2012) Making decisions with unknown sensory reliability. Front Neurosci 6:75
69. Milosavljevic M, Malmaud J, Huth A, Koch C, Rangel A (2010) The Drift Diffusion Model can account for the accuracy and reaction time of value–based choices under high and low time pressure. Judgm Decis Making 5:437
70. Miller GA (2010) Mistreating psychology in the decades of the brain. Perspect Psychol Sci 5:716
71. Insel T (2010) Faulty circuits. Sci Am 302:44
72. Wagenmakers EJ, van der Maas HJL, Grasman PP (2007) Psychon Bull Rev 14:3
73. Logothetis NK (2003) In: Parker A (ed) The physiology of cognitive processes. Oxford University Press, New York
74. Ratcliff R, McKoon G (2008) The diffusion decision model: Theory and data for two–choice decision tasks. Neural Comput 20:873
75. Churchland AK, Ditterich J (in press) New advances in understanding decisions among multiple alternatives. Curr Opin Neurobiol