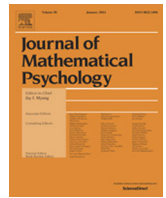




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Variability in behavior that cognitive models do not explain can be linked to neuroimaging data

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HIGHLIGHTS

- Many cognitive models neglect trial-by-trial variability in behavior.
- This can be overcome by assuming variability in model parameters.
- A simple method to effectively capture this variability is introduced.
- The goal is to link variability in model parameters with neuroimaging data.

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ABSTRACT

It is known that behavior is substantially variable even across nearly identical situations. Many cognitive models are not able to explain this *intraindividual* variability but focus on explaining *interindividual* differences captured in model parameters. In sequential sampling models of decision making, for instance, one single threshold parameter value is estimated for every person to quantify how much evidence must be accumulated for committing to a choice. However, this threshold may vary across trials even within subjects and experimental conditions. Neuroimaging tools such as functional magnetic resonance imaging (fMRI) or electroencephalography (EEG) can reveal moment-to-moment fluctuations in the neural system that are likely to contribute to fluctuations in behavior. We propose that neural and behavioral variability could be linked to each other by assuming and estimating trial-by-trial variability in model parameters. To illustrate our proposal, we first highlight recent studies in model-based cognitive neuroscience that have gone beyond correlating model predictions with neuroimaging data. These studies made use of variance in behavior that remained unexplained by cognitive modeling but could be linked to specific fMRI or EEG signals. Second, we specify in a tutorial a novel and efficient approach, how to extract such variance and to apply it to neuroimaging data. Our proposal shows how the variability in behavior and the neural system can provide a fruitful source of theory development in cognitive neuroscience.

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1. Introduction

Cognitive neuroscience and cognitive modeling pursue a common goal, which is to identify the various mechanisms that give rise to observable behavior. It is therefore not surprising that their combination has become an extremely productive research agenda. For example, model-based functional magnetic resonance imaging (fMRI; O'Doherty, Hampton, & Kim, 2007) has been applied to link activation in the brain's reward circuitry, including the ventral striatum and the ventromedial prefrontal

cortex, to the parametric encoding of reward expectations and reward prediction errors (Bartra, McGuire, & Kable, 2013; Clithero & Rangel, 2014; Garrison, Erdeniz, & Done, 2013). Expected values and prediction errors are particularly suitable for neuroimaging data analysis, because they vary on a trial-by-trial basis when using reinforcement learning (RL) paradigms. The predictions of an RL model – that has been fitted to the choice data – are simply regressed against the fMRI data, revealing which brain areas track the development of expected values or prediction errors over the course of the experiment (e.g., Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006; Gläscher, Hampton, & O'Doherty, 2009; Gluth, Rieskamp, & Büchel, 2014; O'Doherty et al., 2004 and Pessiglione et al., 2008).

Importantly, a person will perceive an identical decision situation differently after receiving feedback, which leads to

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learning and consequently to different behavior across trials. In contrast to learning situations, however, many psychological experiments use static environments, and potential changes in cognitive processes from trial to trial are not accounted for. Even an RL model does not predict any trial-by-trial variability, as long as no learning takes place (e.g., if the feedback is fully predictable). In the worst case, some models make deterministic predictions and do not allow accounting for any form of variability. Traditional models of decision making under uncertainty, including expected utility theory (Von Neumann & Morgenstern, 1947), prospect theory (Kahneman & Tversky, 1979), but also some choice heuristics (e.g., Brandstätter, Gigerenzer, & Hertwig, 2006), belong to this category. Applying a naïve error theory allows formulating choice predictions in terms of a probability distribution (Hey, 1995; Loomes & Sugden, 1995; McFadden, 2001; Rieskamp, 2008). Beyond that, sequential sampling models of decision making assume that stochastic sampling of evidence underlies the decision process, which allows probabilistic predictions of response times (Busemeyer & Townsend, 1993; Smith & Ratcliff, 2004). However, even probabilistic choice models make identical probabilistic predictions for identical choice situations, so that if the probability of choosing option A over alternative option B is predicted to be, say, 60% in one trial, it will also be 60% when the same situation is encountered a few trials later. That the subject might actually choose A in the first but B in the second situation (instead of B and then A, or A in both trials, or B in both trials) has to be attributed to unsystematic noise the model cannot explain.

More precisely, when model parameters are assumed to be fixed for specific conditions or persons, variability in behavior is difficult to explain (Lee & Wagenmakers, 2014; Lewandowsky & Farrell, 2011). In sequential sampling models of decision making, for instance, a single decision threshold parameter value is estimated that reflects the amount of evidence required to make a choice (Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006; Smith & Ratcliff, 2004). This parameter might vary across different conditions, for example, when either speed or accuracy is emphasized. But within a single condition the threshold is assumed to be fixed, and its value is usually estimated based on hundreds or even thousands of trials (e.g., Ratcliff & Rouder, 1998). Naturally, the behavior varies across these trials, and the sequential sampling model “explains” this by the variability of the stochastic process of sampling information. However, we argue that the variability in behavior across trials could also be due and explained by the variability of model parameters such as a decision threshold (see also Craigmile, Peruggia, & Van Zandt, 2010 and Zandbelt, Purcell, Palmeri, Logan, & Schall, 2014). Moreover, behavioral variability should in principle be reflected in variability of the recorded brain data (see also Glimcher, 2005). We suggest that the variability of behavior and the neural system could be matched to each other and might offer important insights about the neurocognitive system and the models trying to explain it.

Indeed, recent studies in model-based cognitive neuroscience have tried to exploit this trial-by-trial variability by first contrasting a model’s average predictions with the participants’ actual behavior in single trials (i.e., response times [RTs] and/or choices) and then using this prediction–observation discrepancy to inform the analysis of neuroimaging data (Gluth, Rieskamp, & Büchel, 2012; Gluth, Sommer, Rieskamp, & Büchel, 2015; van Maanen et al., 2011). The central aim of this review and tutorial is to present a generalization of this approach to illustrate its applicability to (almost) any form of cognitive model and (almost) any form of neural or physiological data.

The rest of the article is structured as follows: In Section 2, we summarize neuroimaging studies of human decision making that captured trial-by-trial deviations from model predictions to analyze the brain data as outlined above; in Section 3, we provide

a general formalization of this approach rooted in Bayesian theory, as well as an accompanying example to facilitate understanding; in Section 4 we discuss and exemplify parameter recovery simulations as a precondition for the successful application of our technique; in Section 5 we specify further requirements and recommendations for models and neuroimaging data; Section 6 provides a comparison with alternative ways to test for trial-by-trial effects; finally, Section 7 concludes with a discussion of potential results that can be obtained with this technique and their implications for further developments of theories in cognitive neuroscience.

2. Model-based neuroimaging studies of parameter variability

Whereas reinforcement learning studies exploited the fact that many learning components such as reward expectations, prediction errors, but also learning rates and various forms of uncertainty are naturally changing (Behrens, Woolrich, Walton, & Rushworth, 2007; Boll, Gamer, Gluth, Finsterbusch, & Büchel, 2013; & Kable, 2014; Payzan-LeNestour, Dunne, Bossaerts, & O’Doherty, 2013), models of decision making (including sequential sampling models) face the problem that predictions often remain constant from trial to trial.¹ In fact, observations are assumed to be generated by the same probability distribution (e.g., a Wiener diffusion process) and to be mutually independent; that is, they are independent and identically distributed (i.i.d.) random variables (Luce, 1986). Accordingly, early model-based fMRI studies on perceptual decision making restricted the association of cognitive modeling and brain data to correlations across subject (Forstmann et al., 2008). In particular, Forstmann and colleagues used the linear ballistic accumulator (LBA) model (Brown & Heathcote, 2008) to model choices and RTs in a random dot motion task with different conditions that prioritized speed, accuracy, or neither. The LBA was estimated so as to allow specifying the level of response caution (i.e., the distance between the decision threshold and the upper end of the starting point distribution) in speed and accuracy conditions separately. As expected, subjects were less cautious in the speed condition. At the time when people were instructed to respond quickly or accurately in the upcoming trial, the authors recorded the fMRI signal in the pre-supplementary motor area (pre-SMA) and the caudate nucleus (CN). They reported a negative correlation between the difference in response caution in the speed and accuracy conditions and the difference in fMRI signal in pre-SMA and CN. Their conclusion was that a higher increase in baseline activity in the pre-SMA and CN mediated particularly fast decisions in the speed condition.

Forstmann et al.’s (2008) results clearly indicate an involvement of the pre-SMA and CN in response caution. However, if we consider the possibility that the decision threshold does not stay constant across trials within a specific condition, then the study leaves open whether these brain structures could also be important for threshold adjustments on a trial-by-trial level. The following hypothetical example illustrates the point: The average “brain activity” (across all trials and subjects) in the pre-SMA/CN could be $x_a = 10$ in the accuracy condition and $x_s = 20$ in the speed condition; the average value of response caution parameter could be $\pi_a = 20$ in

¹ Ratcliff’s drift diffusion model assumes across-trial variability in the drift rate, starting point, and non-decision time (Ratcliff, 1978; Ratcliff & McKoon, 2008). However, the model only estimates the “average” amount of across-trial variability and does not specify the amount or direction of variability in single trials. Thus, it makes no trial-by-trial predictions of how the parameter values vary. More recent modeling techniques have been developed to address this point (Turner, van Maanen, & Forstmann, 2015; Wiecki, Sofer, & Frank, 2013), which we discuss in more detail in Section 6.

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