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Models of probabilistic category learning in Parkinson's disease: Strategy use and the effects of L-dopa

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ABSTRACT

Probabilistic category learning (PCL) has become an increasingly popular paradigm to study the brain bases of learning and memory. It has been argued that PCL relies on procedural habit learning, which is impaired in Parkinson's disease (PD). However, as PD patients were typically tested under medication, it is possible that levodopa (L-dopa) caused impaired performance in PCL. We present formal models of rule-based strategy switching in PCL to re-analyse the data from [Jahanshahi, M., Wilkinson, L., Gahir, H., Dharminda, A., & Lagnado, D.A., (2009). Medication impairs probabilistic classification learning in Parkinson's disease. *Manuscript submitted for publication*] comparing PD patients on and off medication (within subjects) to matched controls. Our analysis shows that PD patients followed a similar strategy switch process as controls when off medication, but not when on medication. On medication, PD patients mainly followed a random guessing strategy, with only few switching to the better Single Cue strategies. PD patients on medication and controls made more use of the optimal Multi-Cue strategy. In addition, while controls and PD patients off medication only switched to strategies which did not decrease performance, strategy switches of PD patients on medication were not always directed as such. Finally, results indicated that PD patients on medication responded according to a probability matching strategy indicative of associative learning, while the behaviour of PD patients off medication and controls was consistent with a rule-based hypothesis testing procedure.

1. Introduction

Parkinson's disease (PD) is well known for its characteristic motor symptoms such as rigidity, tremor and akinesia (lack of movement). In addition to these, PD has been associated with a number of cognitive deficits. Dementia is prevalent in PD patients (Aarsland, Zaccai & Brayne, 2005), but there is a range of less severe cognitive symptoms of PD, related to working memory (Owen, Iddon, Hodges, Summers & Robbins, 1997), attention (Filoteo & Maddox, 1999), set-shifting (Cools, Barker, Sahakian & Robbins, 2001b), and procedural learning (Saint-Cyr, Taylor & Lang, 1988). PD patients have also been shown to be impaired in category learning (Ashby, Noble, Filoteo, Waldron & Ell, 2003; Filoteo, Maddox, Ing & Song, 2007; Filoteo, Maddox, Salmon & Song, 2005; Knowlton, Mangels & Squire, 1996; Maddox, Aparicio, Marchant & Ivry, 2005; Shohamy, Meyers, Onlaor & Gluck, 2004). Given the nature of the disease, it may come as no surprise that PD patients show certain learning deficits. PD involves the loss of dopamine producing cells in the substantia nigra pars compacta, resulting in dopamine depletion in the dorsal striatum, extending to other areas such as the ventral striatum and prefrontal cortex as the disease progresses (Cools, 2006). Dopamine is thought to play a crucial role in the flexible control of behaviour in response to environmental demands (Cools, 2006; Nieoullon, 2002). Evidence suggests that phasic dopamine bursts and dips in the striatum code "reward prediction errors" (O'Doherty, Dayan, Schultz, Deichmann, Friston & Dolan, 2004; Schultz, 2002; Schultz, Dayan & Montague, 1997), associated with the presence of an unexpected reward and absence of an expected reward, respectively. Prediction errors are crucial to many learning theories and the disruption of these signals in PD is thus likely to impair learning.

In this article, we restrict our attention to Probabilistic Category Learning (PCL), involving tasks in which stimulus features are

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imperfect predictors of category membership. A popular PCL task is the Weather Prediction Task (WPT, Knowlton, Squire & Gluck, 1994), which asks participants to predict the state of the weather (Rainy, or Fine) based on combinations of four "tarot" cards which are related to the weather with different probabilities. Research with the WPT has provided mixed results. Some studies showed that, compared to healthy controls, PD patients were impaired in early learning (Knowlton et al., 1996; Witt, Nushman & Deuschl, 2002), but to a lesser extent (Knowlton et al., 1996) or not (Witt et al., 2002) in later learning. Other studies found impaired performance throughout the task (Shohamy, Meyers, Grossman, Sage & Gluck, 2004; Shohamy, Meyers, Onlaor et al., 2004; Wilkinson, Lagnado, Quallo & Jahanshahi, 2008). Some studies found no impairment in performance at all (Moody, Bookheimer, Vanek & Knowlton, 2004; Price, 2005).

One explanation of these discrepant findings is that there are different ways in which PCL tasks such as the WPT can be solved, and that these different learning strategies implicate distinct neural circuits. One impetus for the claim of such dissociable learning systems was the finding that amnesic patients showed no (early) impairment in the WPT, whilst being unable to recall certain aspects of the testing episode (Eldridge, Masterman & Knowlton, 2002; Knowlton et al., 1996, 1994). Impaired WPT performance was not accompanied by this lack of declarative memory in PD patients (Knowlton et al., 1996; Sage et al., 2003; Witt et al., 2002). The double dissociation between learning performance and explicit recall has been taken as evidence for the existence of multiple memory systems (Ashby, Alfonso-Reese, Turken & Waldron, 1998; Ashby & Maddox, 2005; Gabrieli, 1998; Knowlton et al., 1996, 1994; Poldrack & Rodriguez, 2004; Shohamy, Meyers, Kalanithi & Gluck, 2008). According to this view, PCL involves an implicit habit learning process which depends on the dorsal striatum, an area unaffected by amnesia. Declarative memory on the other hand involves the medial temporal lobes, an area which is impaired in amnesic, but not PD, patients. Knowlton et al. (1996) suggested that PD patients who did learn in the WPT relied on declarative learning strategies, which is supported by the finding that PD patients showed normal learning in a paired-associate version of the WPT, emphasizing declarative learning by memorization (Shohamy, Meyers, Grossman et al., 2004). This suggests that PD patients have particular problems in learning from feedback to their responses, which can be related to disrupted reward prediction error signals. Neuroimaging studies with healthy individuals have shown increased activity in the striatum and decreased activity in the medial temporal lobes during the normal (feedback based) WPT (Poldrack et al., 2001; Witt et al., 2002). PD patients on the other hand show increased activation in the medial temporal lobes throughout the task, as well as lower activity in the dorsal striatum than controls (Witt et al., 2002). The emerging picture is thus that, due to a disrupted striatal habit learning system, PD patients rely on a qualitatively different learning process, one that is explicit (declarative) rather than implicit (procedural).

Upon closer scrutiny, there is reason to doubt the implicit, habitual nature of PCL. Both healthy (Lagnado, Newell, Kahan & Shanks, 2006) and amnesic (Speekenbrink, Channon & Shanks, 2008) participants have shown explicit insight into the cue–outcome contingencies, thus indicating access to representations of the task environment which should be absent in purely habitual learning. Indeed, there is now considerable evidence that PCL relies at least partially (Meeter, Myers, Shohamy, Hopkins & Gluck, 2006), if not wholly (Lagnado et al., 2006; Newell, Lagnado & Shanks, 2007; Price, 2009), on explicit processes. Furthermore, a recent study failed to replicate the results of Shohamy, Meyers, Grossman et al. (2004). Instead of selective impairment on the feedback-based but normal learning on the paired associate version of the WPT, we found PD patients were impaired on both versions relative to controls (Wilkinson et al., 2008). With the above in mind, it is important to note that previous studies have almost exclusively tested PD patients whilst on medication. The current medication levodopa (L-dopa) is a precursor for dopamine and it raises the dopamine levels in affected areas. Whilst generally effective in reducing motor symptoms, the effects of L-dopa on cognitive functioning are less clear, sometimes improving and sometimes deteriorating cognitive ability (Cools, Barker, Sahakian & Robbins, 2001a; Gotham, Brown & Marsden, 1988; Swainson, Rogers, Sahakian, Summers, Polkey & Robbins, 2000). Evidence suggests that the relation between dopamine and performance follows an "inverted U-shaped" function (Cools, 2006). Increasing dopamine levels can either enhance or lower performance, depending on baseline dopamine levels, implying a possible L-dopa "overdose" effect on relatively spared areas such as the ventral striatum and/or the prefrontal cortex (Cools et al., 2001a; Cools, 2006; Frank, 2005; Gotham et al., 1988). This raises the question whether the impairment in PCL displayed by PD patients is the result of impaired habit learning due to dorsal striatal dysfunction, or of an L-dopa overdose effect on relatively intact areas. As the ventral striatum and prefrontal cortex are thought to support more intentional and representational forms of learning, impaired PCL learning by PD patients on medication may be due to impaired explicit rather than implicit learning processes.

In this article, we will apply a formal modelling framework to assess the nature of PCL in PD and how it is affected by L-dopa. Based on work by Gluck, Shohamy and Myers (2002), we formulate a model of rule-based learning consistent with explicit learning strategies such as hypothesis testing. We contrast it to a model which is more closely related to associative or habitual learning. We apply the models to data from Jahanshahi, Wilkinson, Gahir, Dharminda and Lagnado (submitted for publication), who conducted an experiment in which PD patients performed the WPT both on and off medication (L-dopa). These data allow us to test whether PD patients approach PCL tasks in a different way than healthy controls and whether their learning strategy is affected by L-dopa. If performance in the WPT depends primarily on a habit learning system supported by the dorsal striatum (e.g., Knowlton et al., 1996, 1994), we should expect the associative model to fit control participants better than the rule-based model. We should expect the opposite pattern for PD patients, who must overcome impaired habit learning by relying on declarative strategies. If, on the other hand, performance depends on more explicit processes, we should expect the rule-based model to fit both controls and PD patients better than the associative model. However, if an L-dopa overdose effect impairs these explicit strategies, we might expect the rule-based model to fit poorly to PD patients on medication.

In the following, we will first describe the Weather Prediction Task, which is followed by a brief description of the study conducted by Jahanshahi et al. (submitted for publication). We will then introduce our strategy switch model and describe the different versions that we fitted to the data. In the results section, we first discuss how these models described behaviour in the PD and control group separately, and then investigate group differences in learning strategies.

2. The Weather Prediction Task

In the Weather Prediction Task, participants are asked to predict the state of the weather Y ($1 =$ Fine, $0 =$ Rainy), on the basis of four "tarot cards" x_j (cards with geometrical patterns), which are either presented ($x_j = 1$) or not ($x_j = 0$). Each card is associated with the weather with a different probability. Jahanshahi et al. (submitted for publication) used the version introduced by Gluck et al. (2002), in which card 1 (card 4) is strongly ($p = .8$) associated