ELSEVIER

Neuropsychologia 44 (2006) 1737–1751

NEUROPSYCHOLOGIA

www.elsevier.com/locate/neuropsychologia

Focal putamen lesions impair learning in rule-based, but not information-integration categorization tasks

Shawn W. Ell *, Natalie L. Marchant, Richard B. Ivry

University of California, Berkeley, United States

Received 12 October 2005; received in revised form 27 February 2006; accepted 12 March 2006
Available online 25 April 2006

Abstract

Previous research on the role of the basal ganglia in category learning has focused on patients with Parkinson's and Huntington's disease, neurodegenerative diseases frequently accompanied by additional cortical pathology. The goal of the present study was to extend this work to patients with basal ganglia lesions due to stroke, asking if similar changes in performance would be observed in patients with more focal pathology. Patients with basal ganglia lesions centered in the putamen (6 left side, 1 right side) were tested on rule-based and information-integration visual categorization tasks. In rule-based tasks, it is assumed that participants can learn the category structures through an explicit reasoning process. In information-integration tasks, optimal performance requires the integration of information from two or more stimulus components, and participants are typically unaware of the category rules. Consistent with previous studies involving patients with degenerative disorders of the basal ganglia, the stroke patients were impaired on the rule-based task, and quantitative, model-based analyses indicate that this deficit was due to the inefficient application of decision strategies. In contrast, the patients were unimpaired on the information-integration task. This pattern of results provides converging evidence supporting a role of the basal ganglia and, in particular, the putamen in rule-based category learning.

Keywords: Basal ganglia; Neostriatum; Strategy; Explicit; Implicit

Category learning has been one of the cornerstone areas of study in cognitive psychology. With the emergence of cognitive neuroscience, the neural substrates of this ability have received much attention over the past decade (see Ashby & Spiering, 2004; Keri, 2003 for reviews). The basal ganglia have been a focal point of inquiry in this research, behaviorally (e.g., Knowlton, Mangels, & Squire, 1996; Shohamy, Myers, Onlaor, & Gluck, 2004), computationally (Ashby, Alfonso-Reese, Turken, & Waldron, 1998; Brown, Bullock, & Grossberg, 1999; Frank, 2005), and in neuroimaging studies (Poldrack et al., 2001; Seger & Cincotta, 2002). To date, neuropsychological studies of the role of the basal ganglia in category learning have focused on patients with degenerative disorders of the basal ganglia, and in particular, patients with Parkinson's disease. In the current study, we extend this work by testing patients with focal lesions of the basal ganglia due to stroke.

Testing patients with focal lesions has several advantages compared to those with degenerative disorders. First, unlike Parkinson patients, dopaminergic projections to prefrontal cortex are likely to be normal as long as the lesion excludes the substantia nigra pars compacta, ventral tegmental area, and internal capsule. Second, patients with focal lesions offer a better opportunity to relate structure to function in that one can ask if observed deficits are related to the site of the lesion. Third, they provide an opportunity to evaluate if deficits require bilateral basal ganglia pathology.

An additional goal of the present study is to determine whether focal basal ganglia lesions affect learning in both rule-based and information-integration category learning tasks (Ashby & Ell, 2001). Rule-based tasks are those in which the categories can be learned by an explicit reasoning process. Frequently, the rule that maximizes accuracy (i.e., the optimal rule) can easily be described verbally (Ashby et al., 1998). In many applications, only one stimulus dimension is relevant (e.g., line length), and the participant's task is to identify the relevant dimension and then map the different dimensional values to the relevant categories. Rule-based tasks are assumed to be learned via a hypothesis-testing process that is dependent on working

* Corresponding author at: Cognition and Action Laboratory, Helen Wills Neuroscience Institute and Psychology Department, University of California, 3210 Tolman Hall #1650, Berkeley, CA 94720-1650, United States.
Tel.: +1 510 642 0135; fax: +1 510 642 5293.
E-mail address: shawnell@socrates.berkeley.edu (S.W. Ell).

0028-3932/$ – see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2006.03.018

memory and executive functions (Ashby et al., 1998). Indeed, the Wisconsin Card Sorting task, one of the standard tools for assessing executive function, is in essence a rule-based categorization task.

In contrast, information-integration tasks are those in which accuracy is maximized when information from two or more dimensions (e.g., line length and orientation) is integrated at some pre-decisional stage (Ashby et al., 1998). The type of integration required could take any number of forms, from a weighted combination of the two dimensions (Ashby & Gott, 1988; Garner, 1974) to more holistic processing (e.g., Kemler Nelson, 1993) to the incremental acquisition of stimulus-response associations (Ashby & Waldron, 1999), but the critical point is that integration occurs prior to any decision processes (Ashby et al., 1998). Unlike rule-based tasks, participants have difficulty verbalizing the optimal decision strategy in information-integration tasks, despite being able to successfully learn the categories (Ashby et al., 1998).

Behavioral evidence suggests that qualitatively different systems are engaged during category learning in rule-based and information-integration tasks (see Ashby & Maddox, 2005; Maddox & Ashby, 2004 for reviews). Learning in information-integration tasks is more sensitive to the timing (Maddox, Ashby, & Bohil, 2003) and nature of trial-by-trial feedback (Ashby, Maddox, & Bohil, 2002), and more closely linked to motor systems (Ashby, Ell, & Waldron, 2003). Rule-based tasks are more sensitive to dual task interference (Waldron & Ashby, 2001; Zeithamova & Maddox, in press) and other manipulations designed to tax working memory (Maddox, Filoteo, Hejl, & Ing, 2004).

In contrast to the wealth of behavioral data comparing rule-based and information-integration tasks, there is a paucity of studies investigating the neural substrates of these two tasks. The available neuroimaging data suggest that activity in the basal ganglia is correlated with learning in both tasks (Filoteo, Maddox, Simmons et al., 2005; Nomura et al., in press; Seger & Cincotta, 2002). For instance, Nomura and colleagues observed that successful categorization (i.e., correct–incorrect trials) was correlated with activity in the right body of the caudate nucleus in a rule-based task and bilateral activity in the body and tail of the caudate in an information-integration task.

The role of the basal ganglia in categorization has been the focus of several neuropsychological studies. Patients with Parkinson's disease have consistently been found to be impaired on rule-based tasks (Brown & Marsden, 1988; Cools, van den Bercken, Horstink, van Spaendonck, & Berger, 1984; Downes et al., 1989; Maddox, Aparicio, Marchant, & Ivry, 2005). Interestingly, these studies have all used tasks that required selective attention to a single stimulus dimension in order to maximize accuracy. At least for Parkinson's patients, this detail may be critical as the degree of their impairment increases with the number of irrelevant dimensions (Filoteo, Maddox, Ing, Zizak, & Song, 2005). Moreover, no impairment was observed on a rule-based task that required the participants to attend to all stimulus dimensions (Filoteo, Maddox, Ing, & Song, 2005; Maddox & Filoteo, 2001).

Patients with degenerative disorders of the basal ganglia have been found to be impaired on information-integration tasks as well (Filoteo, Maddox, & Davis, 2001; Filoteo, Maddox, Salmon, & Song, 2005). The information-integration tasks used in these studies comprised two categories and either required the linear or nonlinear integration of the stimulus dimensions. Filoteo et al. (Filoteo, Maddox, Salmon et al., 2005; see also Maddox & Filoteo, 2001) reported an intriguing dissociation in that Parkinson's patients were only impaired on an information-integration task involving a nonlinear decision bound. However, patients with Huntington's disease were impaired in both the linear and nonlinear cases, although the former deficit was limited to the initial training blocks (Filoteo et al., 2001).

Two studies have investigated rule-based and information-integration category learning in the same sample of patients. Ashby and colleagues (Ashby, Noble, Filoteo, Waldron, & Ell, 2003) compared the performance of patients with Parkinson's disease to control participants on rule-based and information-integration tasks. The stimuli comprised four binary-valued dimensions. For successful performance on the rule-based task, participants had to attend to a single relevant dimension and ignore three irrelevant dimensions. Conversely, on the information-integration task, participants had to attend to three dimensions and ignore a single irrelevant dimension. Parkinson's patients were selectively impaired on the rule-based task. Surprisingly, when rule-based and information-integration tasks were equated for the number of relevant dimensions, Parkinson's patients were unimpaired in both tasks (Filoteo, Maddox, Ing, & Song, 2005).

To our knowledge, only one study has investigated the impact of a focal basal ganglia lesion on category learning (Keri et al., 2002). Compared to a group of control participants, a patient with a lesion of the right neostriatum (i.e., caudate and putamen) was impaired on a probabilistic classification task (i.e., the weather prediction task, Knowlton, Squire, & Gluck, 1994). This task is typically considered a type of an information-integration task given that optimal performance requires integrating information from four cues (Ashby & Ell, 2001). However, analyses of individual differences suggests that participants frequently rely upon unidimensional rule-based strategies and memorization (Gluck, Shohamy, & Myers, 2002).

In sum, while the neuropsychological studies indicate that degenerative disorders of the basal ganglia impair category learning, it remains unclear if this deficit extends to both rule-based and information-integration tasks. One problem in comparing performance on rule-based and information-integration tasks is that they frequently differ in terms of difficulty, optimal accuracy, and/or the number of relevant dimensions. Moreover, the literature indicates that various factors influence the degree of the observed impairments even within these two broad classes.

In the current study, we test a group of patients with focal basal ganglia lesions on the rule-based and information-integration categorization tasks introduced by Maddox, Bohil, and Ing (2004). The stimuli were lines that varied in length and orientation, assigned to one of four categories (Fig. 1). We selected stimulus sets such that the two tasks were equated on task difficulty, optimal accuracy, and the number of relevant