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Introduction

Instrumental conditioning involves learning to choose an action that leads to reward. According to the actor-critic model of instrumental conditioning, two distinct components are involved in this process, a "critic" which learns to predict future reward, and an actor which uses a prediction error (PE) signal derived from the critic, to modify its policy so that actions associated with greater long-term reward are chosen more frequently (Dayan & Abbot, 2001; Joel et al., 2002; Montague et al., 1996; Sutton, 1998). A recent neuroimaging study found evidence for neural activity in dorsal and ventral striatum that may relate to the actor and critic components of instrumental conditioning respectively (O'Doherty et al., 2004). However, it is not clear whether such signals are causally related to such learning or merely an epi-phenomenon. The aim of the present study was to determine whether learning in an instrumental conditioning task critically depends on activation of the dorsal striatum. To achieve this, we used an instrumental conditioning task (Friedland, 1998; Joel et al., 2005) in which approx. 50% of normal subjects fail to learn, that is favor the most rewarded action by the end of learning. By exploiting these individual differences in learning efficacy, we aimed to extrapolate the relationship between neural activity in striatum and instrumental learning performance. We hypothesized that regions playing a critical role in instrumental conditioning should be more engaged in those subjects who succeed in learning the task (learners) than in those who fail to learn the task (non-learners).

Methods

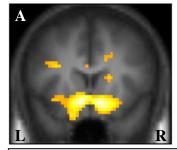
30 subjects (1 discarded) were scanned with fMRI on a GE 3.0T Excite scanner while undergoing the instrumental conditioning procedure. Analysis of fMRI data was performed in SPM2. Subjects' decisions were modeled as a function of previous choices and rewards using a temporal-difference (TD) algorithm. Free parameters (learning rate, softmax temperature, etc.) were selected to optimize the likelihood of the behavioral data, separately for the learners and non-learners groups. Prediction error signals were generated for each subject, convolved with a canonical hemodynamic response function and regressed against each subjects' fMRI data. Subjects were split into groups according to a learning criterion. Group random effects comparisons were conducted between learners and non-learners to determine areas showing enhanced correlations with TD prediction error signals in learners than non-learners. A simple regression analysis was also conducted between the degree of learning in each subject as measured by the learning criterion and the degree of prediction error activity across subjects.

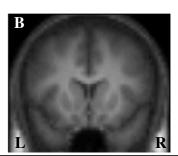
Results

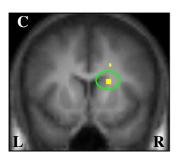
Seventeen out of the 29 subjects met the learning criterion and were categorized as learners, while the remaining subjects were categorized as non-learners. Consistent with our hypothesis, significant correlations with PE signals were found in both the dorsal and ventral striatum in learners at p<0.001 (Fig. 1A). In contrast, only ventral striatum activity was observed in non-learners, and at a lower significance level (p<0.05) (Fig. 1B presents the non-learners at p<0.001). Furthermore, a direct comparison between the two groups revealed that the dorsal striatum was significantly better correlated with PE signals in learners than in non-learners at p<0.001 (Fig. 1C). Furthermore, the simple regression analysis revealed a similar area of dorsal striatum (p<0.005) (Fig. 1D) whereby neural responses to prediction error activity were correlated across subjects with the degree of learning exhibited by those subjects.

Discussion & Conclusion

In this study we exploited between-subject differences in learning efficacy in order to determine whether activity in striatum (in particular the dorsal striatum) is directly related to instrumental conditioning. We found that neural activity in dorsal striatum is significantly better correlated with prediction error signals in learner compared to non-learner subjects. A simple regression analysis demonstrated that the results are not dependent on the specific group categorization procedure used. These results are indicative of the critical role of prediction error signals in dorsal striatum activity during instrumental conditioning. These signals may be generated by afferent dopaminergic inputs into this region.







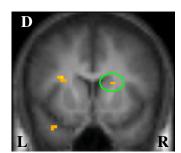


Figure 1: Random effects and correlation analysis showing PE correlations in ventral and dorsal striatum: (A) The Learners group showed significant correlations in bilateral ventral striatum and right dorsal striatum (n=17) (p<0.001); (B) The non-learners group did not show significant correlations in a similar threshold (n=12) (p<0.001). (C) A direct comparison between PE correlated activity in the learners group and the non-learners group, showed enhanced activity in learners compared to non-learners in right dorsal striatum (p<0.001). (D) Simple regression analysis showing correlation in right dorsal striatum between the degree of learning in each subject as measured by the learning criterion and the degree of prediction error activity across subjects (p<0.005).