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Easy to learn, hard to suppress: The impact of learned stimulus–outcome associations on subsequent action control

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ABSTRACT

The inhibition of impulsive response tendencies that conflict with goal-directed action is a key component of executive control. An emerging literature reveals that the proficiency of inhibitory control is modulated by expected or unexpected opportunities to earn reward or avoid punishment. However, less is known about how inhibitory control is impacted by the processing of task-irrelevant stimulus information that has been associated previously with particular outcomes (reward or punishment) or response tendencies (action or inaction). We hypothesized that stimulus features associated with particular action–valence tendencies, even though task irrelevant, would modulate inhibitory control processes. Participants first learned associations between stimulus features (color), actions, and outcomes using an action–valence learning task that orthogonalizes action (action, inaction) and valence (reward, punishment). Next, these stimulus features were embedded in a Simon task as a task-irrelevant stimulus attribute. We analyzed the effects of action–valence associations on the Simon task by means of distributional analysis to reveal the temporal dynamics. Learning patterns replicated previously reported biases; inherent, Pavlovian-like mappings (action–reward, inaction–punishment avoidance) were easier to learn than mappings conflicting with these biases (action–punishment avoidance, inaction–reward). More importantly, results from two experiments demonstrated that the easier to learn, Pavlovian-like action–valence associations interfered with the proficiency of inhibiting impulsive actions in the Simon task. Processing conflicting associations led to more proficient inhibitory control of impulsive actions, similar to Simon trials without any association. Fast impulsive errors were reduced for trials associated with punishment in comparison to reward trials or trials without any valence association. These findings provide insight into the temporal dynamics of task irrelevant information associated with action and valence modulating cognitive control. We discuss putative mechanisms that might explain these interactions.

1. Introduction

The brain's spontaneous processing of irrelevant information can directly affect performance, even to the point of leading behavior astray or interfering drastically with efficient completion of goal-directed actions. This is perhaps best illustrated by so-called conflict tasks, such as Simon (Simon, 1969) or Flanker (Eriksen & Eriksen, 1974) tasks, in which the ineludible processing of irrelevant information in a visual display activates a response tendency that directly conflicts with goal-directed action. These tasks not only permit investigation of the brain's susceptibility to processing irrelevant information and preparing incorrect responses, but also how cognitive control is engaged reactively to inhibit this processing and suppress interference from inappropriate actions that are triggered by irrelevant stimuli.

While these cognitively or perceptually-driven forms of stimulus–response associations are undoubtedly an influential source of conflict in daily life, the processing of other forms of irrelevant information may also contribute to conflict and directly influence cognitive control processes. In particular, stimuli, relevant or irrelevant to behavioral goals, that have been associated with reward and its acquisition (and potentially punishment and its avoidance) are potent modulators of our attention and directly

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engage relevant circuitries involved in reward processing (Anderson, Laurent, & Yantis, 2011a, 2011b; Della Libera & Chelazzi, 2009; Della Libera, Perlato, & Chelazzi, 2011; O'Connor et al., 2015; Raymond & O'Brien, 2009; for a review see Chelazzi, Perlato, Santandrea, & Della Libera, 2013).

The resolution of conflict in Simon and related response conflict tasks involves cognitive control circuitries engaging prefrontal and motor areas of the frontal cortex and the basal ganglia (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Forstmann, van den Wildenberg, & Ridderinkhof, 2008; Ridderinkhof, Forstmann, Wylie, Burle, & van den Wildenberg, 2011). A central component of cognitive control in times of conflict is the inhibition of conflicting response alternatives, which has been linked to frontal projections to basal ganglia that engage the indirect and hyperdirect basal ganglia pathways to brake actions selectively (Aron et al., 2007; Jahfari et al., 2011; Mink & Thach, 1993). Disorders associated with basal ganglia dysfunction produce pronounced deficits in conflict resolution and inhibitory control, and pharmacological (e.g., dopamine) and deep brain stimulation manipulations of basal ganglia function modulate these processes directly (Gillan et al., 2011; Holl, Wilkinson, Tabrizi, Painold, & Jahanshahi, 2013; Worbe et al., 2011; Wylie, Claassen, Kanoff, Ridderinkhof, & van den Wildenberg, 2013; Wylie et al., 2009a, 2009b, 2010, 2012).

These same cortical-basal ganglia circuitries are implicated in reinforcement learning, reward expectation, and the formation of stimulus–action–outcome associations (Alexander, DeLong, & Strick, 1986; Aron et al., 2007; Bogacz & Gurney, 2007; McClure, Berns, & Montague, 2003; Schultz, 2002). In fact, recent theories postulate roles for long-term potentiation and depression in direct and indirect basal ganglia pathways as a potential mechanism for associating action and inaction to reward acquisition and punishment avoidance (Frank & Fossella, 2011; Kravitz & Kreitzer, 2012). While action control and action–outcome processes are generally studied in isolation, emerging ideas suggest a potential interface in basal ganglia circuitries (modulated by dopamine) that integrates action control and valences of action outcomes.

1.1. Current study

The central aim of the current investigation was to determine how response conflict in a Simon task and inhibitory control processes involved to resolve this conflict are influenced by the simultaneous processing of irrelevant information that has been associated previously with reward acquisition or punishment avoidance. Encountering irrelevant stimulus information associated with a particular valence may activate reward (or punishment) processing circuits of the brain directly (i.e. the fronto-striatal connections that are activated when receiving actual reward outcomes, D'Ardenne, McClure, Nystrom, & Cohen, 2008; McClure et al., 2003; O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003; Pagnoni, Zink, Montague, & Berns, 2002), which may in turn impact one's susceptibility to acting on strong motor impulses or interact directly with the control processes engaged to inhibit impulsive response tendencies.

Our general approach was to embed stimulus information associated previously with reward acquisition or punishment avoidance as irrelevant attributes of the visual display in a conventional Simon conflict task. In many reinforcement learning paradigms, only overt actions are associated to reward or punishment outcomes (i.e., instrumental learning) (Frank, Seeberger, & O'Reilly, 2004; O'Doherty et al., 2004; van Wouwe, Ridderinkhof, Band, van den Wildenberg, & Wylie, 2012). However, in many situations, *refraining* from action is necessary for reward acquisition and punishment avoidance. Moreover, learning that only involves selection among overt action alternatives conflicts with inherent biases evoked by punishment (bias to refrain from action) (Cavanagh, Eisenberg, Guitart-Masip, Huys, & Frank, 2013; Everitt, Dickinson, & Robbins, 2001; Freeman, Alvernaz, Tonnesen, Linderman, & Aron, 2015; Freeman, Razhas, & Aron, 2014; Gray & McNaughton, 2000; LeDoux, 1996). To accommodate these issues, we adapted a probabilistic learning task to require either action or inaction to obtain reward or avoid punishment. That is, we orthogonalized valence (reward acquisition, punishment avoidance) and action choice (action, inaction) factors during the learning task so that participants learned each of four color stimuli representing a unique combination of these factors (see design pioneered by Guitart-Masip, Chowdhury, et al., 2012; Guitart-Masip, Huys, et al., 2012).

We tested two alternative predictions based on prior work linking patterns of action–valence learning to specific neural effects. On the one hand, prior work shows that stimulus–action–outcome valences can energize or de-energize motor cortical activity; that is, stimuli associated with reward activate motor cortex, whereas stimuli associated with punishing outcomes decrease motor cortex activity, even before action selection takes place (motivation-to-action 'spillover' account; Chiu, Cools, & Aron, 2014). Based on this pattern, encountering irrelevant stimulus features associated with reward, and particularly reward and action, would be expected to activate motor cortex, which in the context of the Simon task, would potentiate impulsive actions and interfere with inhibitory control. Stimuli associated with punishment avoidance, and particularly punishment avoidance and inaction, would reduce motor cortex activity and produce opposite effects on behavior, thus reducing impulsive errors and making it easier to inhibit impulsive response tendencies triggered in the Simon task.

Alternatively, Guitart-Masip, Chowdhury, et al. (2012) and Guitart-Masip, Huys, et al. (2012) have demonstrated inherent biases during the learning of these action–valence associations that are accompanied by distinct effects on conflict signaling in the brain. Two conditions reflect natural biases between valence and action (i.e., action with reward, inaction with punishment avoidance), whereas two conditions conflict with these natural biases (i.e., action with punishment avoidance, inaction with reward). Learning and implementing the *conflicting* action–valence conditions are accompanied by medial prefrontal oscillatory activity commonly associated with conflict detection or conflict-induced control signals. These signals are absent or substantially reduced when processing the two conditions reflecting natural biases between valence and action (Cavanagh et al., 2013). Since the conflict control system is also engaged by the response conflict produced in the Simon task, encountering inherently conflicting valence–action associations should similarly activate the conflict control system, which would then be expected to either facilitate or, at a minimum, have little impact on the proficiency of conflict control required to resolve the motor conflict in the Simon task. In contrast, encountering inherently natural action–valence associations may interfere with the conflict control system (e.g., take it offline), the effect of which would be a disruption in the engagement of cognitive control to resolve the conflicting motor responses in the Simon task.

Both accounts predict that action–reward associations will likely reduce inhibitory control whereas the accounts differ with respect to predictions for inaction–punishment associations; according to the action–valence conflict account these natural associations might interfere with conflict control. According to the motivation-to-motor 'spillover' account on the other hand, irrelevant information associated with inaction or punishment, and particularly both inaction and punishment, might be expected to induce a bias toward action restraint and facilitate the proficiency of inhibition.