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Suppressing a motivationally-triggered action tendency engages a response control mechanism that prevents future provocation

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ABSTRACT

Reward-predicting stimuli can induce maladaptive behavior by provoking action tendencies that conflict with long-term goals. Earlier, we showed that when human participants were permitted to respond for a reward in the presence of a task-irrelevant, reward-predicting stimulus (i.e. goCS+ trials), the CS+ provoked an action tendency to respond compared to when a non-rewarding CS− stimulus was present (i.e. goCS− trials). However, when participants were not permitted to respond, response suppression was recruited to mitigate the action tendency that was triggered by the motivating CS+ stimulus (i.e. on nogoCS+ trials) (Freeman et al., 2014). Here we tested the hypothesis that repeated response suppression over a motivationally-triggered action tendency would reduce subsequent CS+ provocation. We compared groups of participants who had different proportions of nogoCS+ trials, and we measured CS+ provocation on go trials via reaction time. Our results showed that CS+ provocation on go trials was reduced monotonically as the proportion of nogoCS+ trials increased. Further analysis showed that these group differences were best explained by reduced provocation on goCS+ trials that followed nogoCS+ (compared to nogoCS−) trials. Follow-up experiments using a neurophysiological index of motor activity replicated these effects and also suggested that, following nogoCS+ trials, a response suppression mechanism was in place to help prevent subsequent CS+ provocation. Thus, our results show that performing response suppression in the face of a motivating stimulus not only controls responding at that time, but also prevents provocation in the near future.

1. Introduction

The environment is filled with reward-predicting, Pavlovian stimuli that can motivate our actions (Cavanagh et al., 2013; Gupta and Aron, 2011; Hajcak et al., 2007; Talmi et al., 2008) and bias our decisions (Bray et al., 2008; Chiu et al., 2014; Klein-Flügge and Bestmann, 2012). Such stimuli can be beneficial when obtaining the reward is congruent with our goals (e.g., a marathon runner running faster after passing a picture of a gold medal). Oftentimes, however, appetitive Pavlovian stimuli can motivate actions that conflict with our goals (e.g., a recovering smoker who buys cigarettes after smelling smoke), resulting in "misbehavior of the will" (Dayan et al., 2006). It is therefore essential that, in such circumstances, we learn to control action tendencies that are provoked by appetitive, motivating stimuli.

In an experimental setting, the way in which Pavlovian stimuli motivate our actions towards rewards can be studied by taking advantage of a phenomenon called Pavlovian-to-instrumental transfer (PIT). For a typical PIT task, the participant first undergoes a session of instrumental training and a session of Pavlovian training to develop response-reward and stimulus-reward relationships, respectively. Then, in the Transfer phase, the Pavlovian stimuli are incidentally presented while the participant again engages in instrumental, reward-driven behavior[1] (Holmes et al., 2010). A "PIT effect" occurs when, in the Transfer phase, Pavlovian stimuli previously paired with reward invigorate instrumental responding compared to stimuli not previously paired with reward.

In an earlier study, we used a novel hybrid go-nogo/PIT task to examine how control is implemented over a motivating stimulus that provokes action tendencies (Freeman et al., 2014). This task began with an Instrumental phase where thirsty participants were

[1] The Transfer phase is generally done in extinction, where no rewards are delivered. However, in our adapted version of the PIT task, we continue to reward instrumental behavior in the Transfer phase in order to maximize motivational drive.

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either permitted (go trials) or not permitted (nogo trials) to make instrumental presses for a juice reward. On go trials, participants made quick and repeated presses and received a drop of juice if enough presses were made based on a variable ratio reward schedule. On nogo trials, participants had to refrain from responding and no juice was delivered. If they mistakenly pressed on nogo trials, then a 'Do Not Press' signal was given. After this phase, participants underwent the Pavlovian phase, where they learned to associate a particular color with juice reward and another color with no juice reward (the CS+ and CS−, respectively). In the final phase (Transfer), instrumental responses were made with the motivating (CS+) or non-motivating (CS−) stimulus in the background.

Our main focus of analysis was the Transfer phase, where participants made instrumental responses (go trials) or refrained from responding (nogo trials) in the presence of a motivating (CS+) or a non-motivating (CS−) stimulus. On go trials, instrumental responding was invigorated in the presence of the CS+ compared to the CS− (i.e. the PIT effect). Specifically, we showed that people responded faster on their first press (first press reaction time, RT) and also made more presses for CS+ versus CS−. On nogo trials, there was an increased commission error rate when the CS+ was present. This failure to withhold a response when provoked suggests either that responses were too energized or that a mechanism of response suppression was not always effective in mitigating the action tendencies generated by the CS+.

2. Single-pulse transcranial magnetic stimulation

The behavioral results described above suggest that the CS+ quickly energizes a response, and that, in a nogo context, response activation has to be quickly overcome by a putative response suppression mechanism. To better visualize this activation/suppression process, we previously used single-pulse transcranial magnetic stimulation (spTMS) to probe the underlying motor physiology (see Freeman et al. (2014) for details). On each trial, a single pulse was delivered over the scalp corresponding to the right hand finger muscles. The pulse evoked a response that was recorded with concurrent electromyography (EMG)—the so-called motor evoked potential (MEP). The MEP is an index of corticospinal excitability, which reflects cortical, subcortical, and spinal influences. This method allows one to measure the amount of activation of a muscle representation in the brain even without overt action. When MEPs are reduced beneath a baseline, it is often interpreted as suppression of the response tendency (Cai et al., 2011; Duque et al., 2010). We delivered spTMS in the Transfer phase 250 milliseconds (ms) after go and nogo cues (for CS+ and CS−). On go trials, MEPs were greater for CS+ compared to both CS− and baseline several hundred ms before a response was made, providing further evidence for quick provocation by the CS+. On correct nogo trials, mean MEPs were beneath baseline for CS+ (but not CS−) trials, which suggests that response suppression was triggered by the conflict between the motivationally-triggered activation and the nogo cue. These spTMS results support the hypothesis that response suppression can be recruited to control a motivationally-triggered action tendency.

3. The current study

It is of considerable theoretical and practical significance to develop behavioral methods to reduce and/or prevent the motivational provocation of stimuli. Here we tested the idea that, in the Transfer phase, repeated implementation of putative response suppression on nogoCS+ trials would lead to reduced provocation from the CS+ on go trials. This idea is suggested by recent studies using go-nogo and related paradigms, where withholding responding ("nogo-ing") to reward-related stimuli leads to an apparent decrease in the hedonic value of those stimuli when compared to "going" (Fenske et al., 2005; Ferrey et al., 2012; Houben and Jansen, 2011; Kiss et al., 2008; Wessel et al., 2014). These results have been interpreted as an "inhibitory devaluation", whereby response suppression during nogo trials leads to a reduction in the "value" or "motivational incentive" of reward-related stimuli (Frischen et al., 2012).

In Experiment 1, we tested the hypothesis that response suppression over a motivationally-triggered action tendency would reduce quick provocation from a motivating stimulus by manipulating the number of times that this mechanism was recruited. Specifically, we varied the proportions of nogoCS+ and nogoCS− trials in three independent groups of participants, while holding the proportions of goCS+ and goCS− trials constant. This allowed us to examine if increasing the number of nogoCS+ trials would affect the quick motor energization (reflected in first press RTs) of the CS+ on go trials. Our hypothesis was that, in the group with the highest proportion of nogoCS+ trials, having to perform response suppression more often would lead to a change in the motivating properties of the CS+, which could be examined by comparing RTs for CS+ and CS− on go trials (i.e. the PIT effect). Specifically, we predicted a decreased PIT effect as a function of a greater proportion of nogoCS+ trials. To presage the results, we show that this was the case, as the group PIT effect decreased monotonically with an increasing proportion of nogoCS+ trials. Upon further analysis, it appeared that the best explanation of this result was that nogoCS+ trials reduced provocation if a CS+ (but not a CS−) occurred on the next trial. In three follow-on experiments, we aimed to replicate and further explore these results. We examined trial-by-trial effects, whereby goCS+ followed nogoCS+ or nogoCS− trials. We used spTMS to test when in time, and how, the response suppression on nogoCS+ putatively affects the next trial.

4. Experiment 1

4.1. Method

4.1.1. Participants

Sixty-two undergraduates (twenty males) from the University of California, San Diego participated for course credit (mean age=20.51, SD=1.79). All reported normal or corrected-to-normal visual acuity and provided written informed consent according to a local institutional review board protocol. Data from one participant was excluded due to a failure to properly understand the task and data from another participant was excluded due to a technical malfunction with the juice pump.

4.1.2. Stimuli and procedure

Participants were instructed to abstain from all liquids for a minimum of three hours before arriving at the lab. Upon arrival, each participant completed a pre-experiment questionnaire that surveyed (1) the number of hours since the last consumption of liquid, (2) the type of juice that the participant preferred to consume throughout the experiment (there were four possible juice types: peach Snapple, apple juice, orange juice, and fruit punch), (3) the participant's thirst level (1–7 Likert scale; 1 – Not at all, 7 – Extremely), (4) how much the participant liked the juice that he or she selected (1–7 Likert scale; 1 – Very little, 7 – Very much), and (5) how much the participant wanted the juice at that moment (1–7 Likert scale; 1 – Not at all, 7 – A lot). To proceed with the experiment, a rating of 5 or higher was required for the "wanting of