Behavioural Brain Research 283 (2015) 121–138

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr

Research report

Testing the role of reward and punishment sensitivity in avoidance behavior: A computational modeling approach

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HIGHLIGHTS

- A reinforcement-learning model successfully simulated human avoidance behavior.
- Distinct reward and punishment sensitivity ratio might underlie sex differences.
- Distinct punishment sensitivity might underlie inhibited temperament differences.
- Attenuating effect of safety-signals is due to the competing approach response.
- Safety-signals might be used in cognitive-behavior therapies to reduce avoidance.

ARTICLE INFO

Article history:
Received 9 September 2014
Received in revised form 12 January 2015
Accepted 20 January 2015
Available online 29 January 2015

Keywords:
Avoidance
Computational model
Reinforcement learning
Anxiety vulnerability
Individual difference
Safety-signal

ABSTRACT

Exaggerated avoidance behavior is a predominant symptom in all anxiety disorders and its degree often parallels the development and persistence of these conditions. Both human and non-human animal studies suggest that individual differences as well as various contextual cues may impact avoidance behavior. Specifically, we have recently shown that female sex and inhibited temperament, two anxiety vulnerability factors, are associated with greater duration and rate of the avoidance behavior, as demonstrated on a computer-based task closely related to common rodent avoidance paradigms. We have also demonstrated that avoidance is attenuated by the administration of explicit visual signals during "non-threat" periods (i.e., safety signals). Here, we use a reinforcement-learning network model to investigate the underlying mechanisms of these empirical findings, with a special focus on distinct reward and punishment sensitivities. Model simulations suggest that sex and inhibited temperament are associated with specific aspects of these sensitivities. Specifically, differences in relative sensitivity to reward and punishment might underlie the longer avoidance duration demonstrated by females, whereas higher sensitivity to punishment might underlie the higher avoidance rate demonstrated by inhibited individuals. Simulations also suggest that safety signals attenuate avoidance behavior by strengthening the competing approach response. Lastly, several predictions generated by the model suggest that extinction-based cognitive-behavioral therapies might benefit from the use of safety signals, especially if given to individuals with high reward sensitivity and during longer safe periods. Overall, this study is the first to suggest cognitive mechanisms underlying the greater avoidance behavior observed in healthy individuals with different anxiety vulnerabilities.

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http://dx.doi.org/10.1016/j.bbr.2015.01.033
0166-4328/

1. Introduction

Avoidance is defined as a behavior that causes the omission of aversive events. Avoidance behavior in response to a cue signaling an upcoming aversive event is usually adaptive and serves to protect one from harm, but exaggerated avoidance behavior is a predominant symptom in all anxiety disorders [1], and its severity parallels the development and persistence of these disorders [2–6]. To date, the literature on avoidance behavior is based mainly on rodent studies where neutral signals (warning signals; e.g., tones) predict the occurrence of aversive events (e.g., electric shocks), and the animal learns a predetermined response (e.g., lever-press) to overcome these events. Responding during the aversive event results in its termination (escape response; ER), while responding during the warning signal prevents the occurrence of the aversive event (avoidance response; AR).

1.1. Empirical work in human subjects

Some attempts to operationalize human avoidance behavior have used an operant fear-conditioning framework in which the subject makes responses to avoid mild aversive events ("unpleasant but bearable" electric shocks; e.g., [7,8]). However, since such stimuli are by definition not highly aversive, the generality of the findings is limited; on the other hand, the use of highly aversive (e.g., painful and distressing) stimuli would have serious ethical and practical constraints. Studies that attempt to address how humans avoid truly painful and/or distressing stimuli have instead tended to rely on self-report questionnaires, which ask subjects to report how often they manifest different types of avoidance behaviors in response to real-world stimuli and events (e.g., [9,10]). Another line of research employs computer-based tasks to examine avoidance of aversive feedback (e.g., point loss). In these paradigms, the subject controls a spaceship, attempts to gain reward (point gain) by shooting at enemy spaceships, and learns to avoid aversive on-screen events (point loss). These tasks have been successfully shown to assess different aspects of avoidance behavior, such as passive and active avoidance ([11,12], respectively), effects of different reinforcement contingencies and contextual variables [13], as well as discrimination learning and latent inhibition [14].

We have recently extended one of these tasks (by [12]) to test the acquisition of escape-avoidance behavior in healthy young adults (Fig. 1; [15]). Briefly, in this task participants controlled a spaceship located at the bottom of the screen and were instructed to maximize their score. Participants could learn that a reward (one point) could be obtained by shooting and destroying an enemy spaceship that was moving on the screen. Every 20 s, a signal (a colored rectangle at the top of the screen) appeared for 5 s. Depending on its color, the signal could be a warning signal (W+) that was followed by an aversive event, or a control signal (W−) that was not associated with any event. The aversive event was a bomb that appeared at the center of the screen for 5 s, during which the participant's spaceship was exploded and a maximum of 30 points could be lost. On warning trials, W+ appeared (warning period), followed by the bomb period, which in turn was followed by a 10-s intertrial interval (ITI) during which no signal/bomb occurred. On control trials, W− appeared (control period), followed by a longer 15-s ITI. Participants could learn to protect themselves from the aversive event by moving their spaceship to a specific "safe area" on the screen ("hiding"). However, while in the safe area, it was impossible to shoot the enemy spaceship and obtain reward. Subjects who entered the safe area during the warning period and remained there throughout the bomb period avoided all point loss on that trial (AR); subjects who entered the safe area after the bomb period began were able to escape that point loss (ER). At the beginning of the experiment, participants were given 1 min of practice time, during which they could shoot the enemy spaceship but no signal or bomb appeared.

Sheynin et al. [15] used several variables to describe the escape-avoidance behavior on the computer-based task. First, *hiding duration* indicated the percentage of time spent hiding during the warning period, the control period and the bomb period. Hiding during the bomb period represented an ER and terminated point loss. Hiding during the warning period represented avoidance behavior and could completely prevent any point loss; if the participant emerged from hiding before the end of the bomb period, point loss resumed and response was not recorded as an AR. In addition, Sheynin et al. defined two variables to describe specific aspects of avoidance: *AR rate* – percentage of acquisition trials on which an AR was made and *AR duration* – percentage of the warning period during which the participant's spaceship was hidden, averaged across trials where an AR was made. Longer AR duration indicated that a participant made a response earlier during the warning period and remained hiding longer overall on that trial. In Sheynin et al.'s [15] initial study with the spaceship task, the vast majority of the participants learned the ER, while most of them also learned to completely avoid point loss by performing an AR. This pattern is consistent with what is generally reported in the rodent literature on avoidance learning (e.g., [16]).

In addition to providing a framework to operationalize human avoidance behavior, Sheynin et al. [15] tested associations of avoidance behavior with individual differences and specifically, those that confer anxiety vulnerability. A large animal literature has demonstrated the effect of strain and sex on active avoidance behavior in rodents. Specifically, female sex and inhibited temperament (i.e., behavioral inhibition in response to novel or aversive stimuli) have been associated with greater avoidance behavior in rodents (e.g., [16,17]). Since both female sex and inhibited temperament are vulnerability factors for anxiety disorders ([18,19], respectively), these observations suggested that greater avoidance behavior might mediate vulnerability to anxiety disorders in humans. Indeed, by using the described spaceship avoidance task, Sheynin et al. have found the same facilitated AR pattern in vulnerable young adults. Interestingly, Sheynin et al. [15] also reported a double dissociation of sex and temperament. Specifically, although males and females showed similar AR rate, females had longer AR duration, meaning they tended to spent more of the warning period hiding in the safe areas. On the other hand, inhibited participants had higher AR rate than uninhibited participants, with no difference in AR duration. Together, these findings suggested differential vulnerability pathways associated with sex and temperament.

As a follow-up study, Sheynin et al. [20] extended the spaceship task to eliminate control trials and to include an extinction phase, where W+ was not followed by an aversive event (bomb and point loss). Importantly, impaired extinction learning characterizes anxiety disorders, as well as post-traumatic stress disorder, and is reflected in patients' tendency to keep emitting ARs, although aversive outcomes no longer occur [21]. Results from the acquisition phase on the spaceship task were similar to those of the prior study [15], in that females showed longer AR duration than males; females were also slower to extinguish the avoidance behavior than males (shown by longer hiding duration during the warning period on extinction trials), an effect parallel to the delayed avoidance extinction in animal models of anxiety vulnerability [17].

Sheynin et al. [20] also used the spaceship task to explore the effect of safety signals (SSs; signals associated with non-threat periods), which were shown to modulate avoidance behavior in rodents (e.g., [22–24]; for review, see [20]). Participants were divided into two groups given different versions of the spaceship task – "with-SS" and "without-SS". Participants in the "with-SS" group were administered an SS during the ITI on acquisition trials; the SS took the form of two background lights at the two