Learning and Motivation 59 (2017) 27–37

Contents lists available at ScienceDirect

Learning and Motivation

journal homepage: www.elsevier.com/locate/l&m

Conditioned inhibition in the spatial domain in humans and rats

Edward S. Redhead*, Wai Chan

University of Southampton, United Kingdom

ARTICLE INFO

Keywords:
Spatial learning
Associative learning
Conditioned inhibition
Comparative psychology

ABSTRACT

Spatial learning has been shown to follow associative rules by demonstrations of blocking and overshadowing in both watermazes with rats and virtual watermazes with humans. To examine whether Conditioned Inhibition (CI) can also be demonstrated in a real and virtual watermaze task, two studies were run, one with rats and one with humans. In separate training trials, Beacons A and B marked the position of a platform in quadrant X of circular watermaze (AX +/BX+). In subsequent inhibitory training trials, Beacon A was placed in quadrant Y with no platform present (AY−). To test for any CI of Y, in two probe trials B was suspended above either quadrant Y (BY) or novel quadrant Z (BZ). Time spent under B was recorded in both trials. In both animal and human studies, during no platform probe trials, latencies to reach Beacon B were longer and less time was spent under the beacon when it was suspended in quadrant Y, where inhibitory training had previously taken place (AY− trials), than when it was hung in the novel quadrant Z. Results suggest that quadrant Y had become a conditioned inhibitor strengthening claims that learning in the spatial domain follows the rules of associative models.

1. Introduction

Blocking one element of a compound from forming an association with an unconditioned stimulus by pre-conditioning the other element is predicted by associative learning models such as the Rescorla-Wagner model (1972). The Rescorla-Wagner model assumes that elements in a compound compete to gain associative strength when paired with an unconditioned stimulus. If the preconditioned element has already gained all of the associative strength then the second element cannot gain any strength. Blocking has been demonstrated in the spatial domain both with rats in watermazes (Redhead, Roberts, Good, & Pearce, 1997) and with human participants performing equivalent computer generated watermaze tasks (Redhead, Hamilton, Parker, Chan, & Allison, 2013; Wilson & Alexander, 2008). Chamizo (2003) and Miller and Shettleworth (2007) have suggested that such demonstrations illustrate that learning in a spatial domain is governed by a general process relying on elements competing for associative strength which is predicted by associative models like the Rescorla-Wagner model. However, such blocking of elements might be equally explained by attentional processes, whereby the participants only attend to the preconditioned element. A phenomenon within associative learning more difficult to explain via attentional processes is conditioned inhibition (CI). The aim of this paper is to test whether CI can be demonstrated in a spatial domain with both rats and humans and in a way that can only be predicted by associative models.

In a typical CI experiment (Rescorla, 1969), a stimulus (Y) is paired with a second stimulus which has been previously associated with a US (A+). In the presence of Y, A is no longer associated with the US (AY−), leading to Y becoming a conditioned inhibitor (Mackintosh, 1983). CI of Y is demonstrated by summation and retardation tests (Rescorla, 1969). In a summation test, a reduced response to a second conditioned stimulus (B+) in the presence of Y (BY) compared to the response to B in the presence of a novel stimulus Z (BZ) illustrates conditioned inhibition. Summation effects have been demonstrated with various species and methods, for

* Corresponding author at: School of Psychology, University of Southampton, Highfield, Southampton SO17 1BJ, United Kingdom.
E-mail address: er2@soton.ac.uk (E.S. Redhead).

http://dx.doi.org/10.1016/j.lmot.2017.08.001
Received 31 March 2017; Received in revised form 6 August 2017; Accepted 7 August 2017
Available online 18 August 2017

example with key-pecking in pigeons (Wessels, 1973) and with food aversion in rats (Taukulis & Revusky, 1975). In a retardation test, prior inhibitory conditioning of a CS retards subsequent excitatory conditioning to that CS. Therefore, conditioning to Y+ should be slower compared to excitatory conditioning to a previously novel stimulus. Again retardation has been demonstrated with various species and methods, for example with salivation conditioning in dogs (Konorski & Szwejkowska, 1952) and with eyelid conditioning in rabbits (Marchant, Mis, & Moore, 1972).

However, there have been mixed results from summation and retardation tests following CI training in humans. For example, Artigas, Chamizo, and Peris (2001) demonstrated both summation and retardation following conditioned inhibition of auditory cues, and Thurston and Cassaday (2015) demonstrated summation and retardation in a CI paradigm with visual cues from the International Affective Picture System (IAPS). Grillon and Ameli (2001), on the other hand, found no evidence of summation following CI training of fear-potentiated startle and skin conductance in humans.

In the current studies, CI was tested in a spatial domain by placing a beacon (A) above the platform in quadrant X of a circular watermaze (AX+). In subsequent inhibitory training trials, Beacon A was placed in quadrant Y with no platform present (AY−). To test for any CI of Y, another beacon B, which had previously only been used in trials with the platform present (BX+), was suspended above either quadrant Y (BY) or novel quadrant Z (BZ) where the platform had never been placed during training. If quadrant Y had become inhibitory it would be expected that time to approach Beacon B would be longer when it was above quadrant Y compared to the novel quadrant Z. In subsequent retardation tests the rats and humans were trained to locate a hidden platform in either quadrant Y or the novel quadrant Z. Again, if Y had become a conditioned inhibitor it would be expected that the number of trials to learn the platform is in quadrant Y would be more than if the platform was in the novel quadrant Z.

Horne and Pearce (2010) and Sansa, Rodrigo, Santamaría, Manteiga, and Chamizo (2009) have demonstrated CI within the watermaze using rats, suggesting that, at least with rats, CI in the spatial domain is governed by associative processes. There are other ways to explain CI without recourse to the competitive associative learning predicted by the Rescorla-Wagner model (1975). For example Amsel and Roussel (1952) suggested that an inhibitory stimulus such as Y, rather than becoming inhibitory in order to counter the associative strength of A, might simply induce avoidant behavior due to the omission of a predicted appetitive reinforcer. One way to test whether the CI seen in Horne and Pearce (2010) and in Sansa et al. (2009) was due simply to avoidant behavior would be to present a trial with Y alone following the CI training. If Y is inhibitory due to the associative strength of A, as predicted by the Rescorla-Wagner model, then in the absence of A there should be no avoidance of Y. The current paper will seek to extend the findings of Horne and Pearce (2010) and Sansa et al. (2009) by presenting Y alone following CI training.

Experiment 1 examined CI with rats in a watermaze similar to those used by Horne and Pearce (2010) and Sansa et al. (2009). The current study also differed from the previous studies as to the type of stimuli that were trained as conditioned inhibitors. In the previous studies, specific landmarks were only present on trials with no platform and thus became inhibitory. In the current study, it was the location of the landmark which became inhibitory, as no platform was present on trials when the landmark was in the SW corner. Experiment 2 will further seek to extend the generality of processes governing CI in the spatial domain by testing for CI in humans with a virtual watermaze.

1.1. Experiment 1

1.1.1. Method

1.1.1.1. Participants. Twenty four male Lister-Hooded rats weighing 248–361 g were used in this study, 12 in the novel group, 12 in the inhibitory group. They were approximately 4 months old at the start of this study. Animals were housed in cages of 3–6 with a 12/12 h light/dark cycle and were given free access to food and water. Initially the rats were handled for approximately 1 h per cage over 6 days to minimise the effects of handling stress on performance. Experiments were carried out in accordance with the current British Home Office guidelines, and with consent of the University of Southampton Bioethics Committee. All attempts were made to reduce the number of animals and the degree of suffering.

1.1.1.2. Materials and apparatus. A watermaze was used to assess spatial learning. A white circular plastic pool 2 m in diameter was placed in the centre of a 4 m × 6 m room with white walls. The pool was filled with water, at 23 °C ± 1 °C, and 1 l of milk (to make it opaque) to a depth of approximately 270 mm. The water and milk were changed daily. A 10 × 10 cm circular white platform was used which was always 2.5 cm below the water. The pool was illuminated from above by two strip lights, and visual cues in the room were kept constant throughout the experiment. In the centre of the South wall at a height 2 m, there was a predominantly blue poster (0.5 m × 1 m). In the corner of the north wall was the green door to the room. In the west corner, a 1.8 m × 0.6 m screen was placed 1 m from the pool. Along the length of the East wall was a shelf at a height of 1.5 m. A video camera (Hi-resolution B/W CCD camera, Sanyo) with a wide-angle lens (1.8–3.6 mm, 1:1:6, 1/3", CS, Computer) was fixed 1.5 m above the centre of the pool. During trials, the experimenter sat behind a screen in the south east corner of the room and observed the activity of the rat on a television monitor. For test trials, the video image of the rat's movements was digitized with a Dazzle digital video creator, stored in MPEG 1 format, and then analysed with Ethovision video tracking software (version 3.0, Noldus).

Beacons were hung from the ceiling 30 cm above the water surface using black fishing wire. Beacon A was a red and yellow spotted ball (10 cm diameter) and Beacon B was a black and white striped tube (5 cm diameter, 10 cm in length) (Fig. 1).

1.1.1.3. Procedure. Training and testing took place over 20 days. Rats were transported to the test room four at a time in a box that was placed on the floor in the northwest (NW) corner of the room. Four trials were given on days 1–5. The platform, with Beacon A suspended above, was placed in one of two different locations, which were on the midpoints of the radii pointing NW, through