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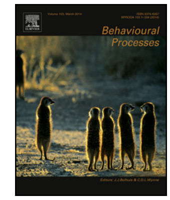

The effect of the amount of blocking cue training on blocking of appetitive conditioning in mice

David J. Sanderson*, William S. Jones, Joseph M. Austen

Department of Psychology, Durham University, South Road, Science Site, Durham, DH1 3LE, UK

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ABSTRACT

Conditioning of a target cue is blocked when it occurs in compound with another cue (blocking cue) that has already received conditioning. Although blocking of appetitive conditioning is commonly used in rodents as a test of selective learning, it has been demonstrated rarely in mice. In order to investigate the conditions that result in blocking in mice two studies tested the effect of the extent of prior blocking cue training on blocking of appetitive conditioning. Mice received either 80 or 200 trials of blocking cue training prior to compound conditioning. A control group received only compound training. Experiment 1 assessed the ability of a visual cue to block conditioning to an auditory target cue. Exposure to the context and the unconditioned stimulus, sucrose pellets, was equated across groups. Blocking was evident in mice that received 200, but not 80 training trials with the visual blocking cue. Responding to the blocking cue was similar across groups. Experiment 2 assessed the ability of an auditory cue to block conditioning to a visual target cue. Blocking was evident in mice trained with 80 and 200 auditory blocking cue trials. The results demonstrate that the strength of blocking in mice is dependent on the modality and experience of the blocking cue. Furthermore, prolonged training of the blocking cue after asymptotic levels of conditioned responding have been reached is necessary for blocking to occur under certain conditions suggesting that the strength of conditioned responding is a limited measure of learning.

1. Introduction

In a conditioning procedure a cue that has been paired with an unconditioned stimulus (US) may fail to elicit conditioned responding if the cue has been conditioned in compound with another cue that has previously been paired with the unconditioned stimulus (Kamin, 1969). This blocking effect provides an example of the failure of temporal contiguity between events to be sufficient for conditioning. It also demonstrates that there is competition between cues that may reflect selective learning, through changes in processing of the unconditioned stimulus (Rescorla and Wagner, 1972) or attention paid to the different conditioned stimuli (Pearce and Hall, 1980; Mackintosh, 1975). Alternatively it may reflect a failure to behaviourally express learning (Stout and Miller, 2007).

Blocking has been demonstrated in numerous species and conditioning procedures (e.g., fear conditioning in rats, Kamin, 1969; autoshaping in pigeons, Leyland and Mackintosh, 1978; odour conditioning in snails, Prados et al., 2013; conditioning of the nictitating membrane response in rabbits, Solomon, 1977; electrodermal conditioning in humans, Hinchy et al., 1995). However, surprisingly, considering the widespread use of mice for assessing the neural basis of learning, there are few examples of blocking in mice (Bonardi et al., 2010). One of the most common ways of assessing learning in rodents is by appetitive conditioning of magazine approach behaviour, in which pairing a cue with food reward (e.g., a sucrose pellet) results in rodents making anticipatory head entries, during the conditioned stimulus (CS), into the magazine, where food is dispensed. To our knowledge, a study by Bonardi et al. (2010) is the only study reporting blocking of appetitive conditioning in mice. In that study mice received 90 conditioning trials with a 20 s light before receiving conditioning with a compound of the light and a clicker stimulus. A control group received only training with the clicker and light compound. At test mice that received the light conditioning trials showed lower levels of magazine approach behaviour to the clicker compared to the control group.

Given the scarcity of evidence for blocking in mice the aim of the present study was to extend the findings of Bonardi et al. (2010) by examining one of the key parameters in determining whether a conditioning procedure will yield a blocking effect. In two experiments the number of conditioning trials with the blocking cue, prior to compound conditioning, was manipulated. Many

* Corresponding author. Fax: +44 1913343240.
E-mail address: david.sanderson@durham.ac.uk (D.J. Sanderson).

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Table 1
Design of experiment 1.

	Stage 1 (Sessions 1–12)	Stage 2 (Sessions 13–20)	Stage 3 (Sessions 21–28, 31–32)	Test
Blocking(200 trials)	A+	A+	AX+	X
Blocking (80 trials)	B+	A+	AX+	X
Control	B+	B+	AX+	X

Note. Stimulus A was a 10 s presentation of a house light and X was a 10 s presentation a noise. For half of the mice stimulus B was a 10 s clicker and for the other half it was a 10 s presentation of flashing LEDs.

theories of learning assume that the extent of blocking will be a function of the number of blocking cue conditioning trials (e.g., Rescorla and Wagner, 1972), and that blocking will be maximal if the blocking cue has acquired the maximum level of associative strength. However, while models of learning such as Rescorla and Wagner (1972) assume a direct relationship between associative strength and performance (e.g., asymptotic levels of conditioned responding indicate maximum levels of learning), it is likely the case that conditioned responding is not a pure measure of learning. For example, by using particular probe tests it is possible to demonstrate that levels of learning continue to increase beyond the point that asymptotic levels of conditioned responding have been achieved (St. Claire-Smith and Mackintosh, 1974). In the study by St. Claire-Smith and Mackintosh (1974) it was found that although a compound of a tone and a light elicited asymptotic levels of conditioned fear, further pairings of the compound with shock increased the conditioned response to the tone and light when each stimulus was tested separately. Such dissociations between performance and learning have been found in other circumstances. For example, Holland and Rescorla (1975) trained a light to predict the occurrence of food (first-order conditioning) and then subsequently paired a clicker with the light (second-order conditioning). It was found that the clicker produced greater conditioned responding than the light despite the fact that it had not been paired with food. Therefore, although the light was not capable of eliciting strong conditioned responding itself, it had acquired a substantial amount of associative strength to support second-order conditioning of the clicker. Other studies have also found similar dissociations that suggest the strength of the conditioned response fails to convey the information that is acquired by the CS. For example, a backward conditioned cue elicits poor conditioned responding, but is a more effective second-order conditioning cue than a forward conditioned stimulus (Barnet et al., 1997). Similarly a trace conditioned stimulus that elicits weak responding can support stronger second-order conditioning than a cue with a shorter CS-US interval (Lin and Honey, 2011). These results demonstrate that the level of conditioned responding elicited by a cue is potentially a poor index of learning.

In the present study mice either received 80 trials or 200 trials of training with the blocking cue prior to compound conditioning. We have previously observed (in unpublished studies) that 80 trials with a 10 s CS (10 trials per daily session with an inter-trial interval of 240 s, CS offset to CS onset) typically yields asymptotic levels of conditioned responding, regardless of the modality (visual or auditory) of the CS. Therefore, for the mice that received 200 trials conditioning should continue substantially past the amount of trials sufficient to elicit maximum performance. In Experiment 1 we tested the ability of a visual cue to block conditioning of an auditory cue, similar to the procedure used by Bonardi et al. (2010). In Experiment 2 we tested the ability of an auditory cue to block conditioning of a visual cue. Given that there is evidence showing that auditory cues elicit greater levels of magazine activity than visual cues (Holland, 1977) it is possible that the parameters that determine blocking may differ when a visual cue is used to block an auditory cue and vice versa.

2. Method

2.1. Subjects

Experimentally naive female C57BL/6J/Ola mice obtained from Charles River, UK were used. Mice were caged in groups of four, in a temperature controlled housing room (light–dark cycle: 0800–2000). The mice were approximately 10 weeks old and a mean weight of 18.9 g (range = 16.8–21.4 g) at the start of testing. Mice were initially allowed free access to food, but one week prior to training the weights of the mice were reduced, by receiving a restricted diet, and then subsequently maintained at 85% of their free-feeding weights. Mice were tested during the light period between 10 am and 4 pm. Throughout testing mice had ad libitum access to water in their home cages. All procedures were in accordance with the United Kingdom Animals Scientific Procedures Act (1986), under project license number PPL 70/7785.

2.2. Apparatus

Eight identical operant chambers (15.9 × 14.0 × 12.7 cm; ENV-307A, Med Associates), enclosed in sound-attenuating cubicles (ENV-022 V, Med Associates), controlled by Med-PC IV software were used. The front and back walls and the ceiling of each chamber were made from clear Perspex and the sidewalls were made from aluminium. The floor was a grid of stainless steel rods (0.32 cm diameter) each separated by 0.79 cm. Sucrose pellets (14 mg TestDiet, ETH) could be dispensed into a magazine (2.9 × 2.5 × 1.9 cm; ENV-303 M, Med Associates) located in the centre of one of the sidewalls. Breaks in an infrared beam (ENV-303HDM, Med Associates) across the bottom of the entrance to the magazine were used to measure the number of magazine head entries at a resolution of 0.1 s. White noise (ENV-325SM, Med Associates) could be emitted from a speaker (ENV-324 M, Med Associates) located at the top right corner of the wall opposite the magazine. A clicker (ENV-335 M, Med Associates) was located on the exterior top left corner of the wall opposite the magazine. A 28 V, 100 mA house light (ENV-315 M, Med Associates) was located next to the speaker in the centre of the wall. Presentation of the house light resulted in illumination of the chamber. Two LEDs (ENV-321 M, Med Associates) were positioned to the left and the right, above the magazine. Presentation of the LEDs resulted in limited, localised illumination. A fan (ENV-025AC) was positioned above the left LED and was turned on during sessions.

2.3. Procedure

2.3.1. Experiment 1—blocking of an auditory cue

Forty-eight mice were run in two separate cohorts (24 each). Mice in both cohorts were randomly allocated to one of three groups: Blocking-80 trials, Blocking-200 trials, Control. There were eight mice per group, per cohort. The design of Experiment 1 is described in Table 1.

Stage 1. Mice received 12 sessions (one per day) of training with a 10 s CS (either cue A or B) that terminated in the presentation of a sucrose pellet. Each session contained 10 trials, with a variable