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Blocking in rats, humans and snails using a within-subjects design

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ABSTRACT

The present research investigated the blocking effect in three different species, rats, humans and snails in formally equivalent tasks using a within-subjects design. Experiment 1 demonstrated the blocking effect in a context-flavour aversive conditioning preparation in rats: Animals failed to associate a flavour with an illness episode when it was presented in a context in which the illness was already predicted by other cues. Experiment 2 replicated this blocking effect in humans assessing their ability to learn a goal location in a virtual environment: Participants failed to learn the location of the goal in reference to a spatial cue presented alongside other pre-trained spatial cues that already indicated its location. Finally, in Experiment 3, snails failed to associate an odour with the presentation of food in the presence of other odours that already reliably predicted its presentation. The present study offers a start point for systematic comparisons between vertebrate and invertebrate species in formally equivalent tasks that produce univocal demonstrations of the blocking effect.

1. Introduction

Learning is a widespread ability that helps individuals from different animal species to better adapt to their changing environments and benefit from experience. It is uncertain, however, whether learning in different animal groups is ruled by the same general principles. One way to address this important question would be to systematically compare the learning abilities of animals located at widely separated points in the phylogenetic tree in standardized situations appropriate to their diverse sensory-motor capacities (e.g., Bitterman, 1960, 1975).

The most thoroughly studied form of learning is Pavlovian or classical conditioning (Shettleworth, 2010). By allowing animals to anticipate important events, Pavlovian conditioning can be seen as a hugely valuable survival tool. Although most of the research has used vertebrate species, Pavlovian conditioning has also been observed in a few invertebrate species, suggesting that this survival tool is phylogenetically widespread. Traditionally, Pavlovian conditioning was thought to depend upon a relatively simple set of mechanisms which could link, in a Hebbian way (Hebb, 1949), the conditioned stimulus (CS) and the unconditioned stimulus (US) whenever they are presented together (or very closely) in the organism's environment. Research has shown, however, that some instances of conditioning have complex and interesting cognitive content. For example, training with one elemental conditioned stimulus A paired with a US, + (A+ training), before training of a compound containing the pre-trained element, AB+ (where B refers to a novel CS), fails to establish the new (and redundant) B element as an effective conditioned stimulus. This blocking effect (first reported by Kamin, 1969, in experiments using rats) clearly shows that co-occurrence of two events (B and the US in this case) is not enough to promote effective Pavlovian conditioning.

The research of the mechanisms behind blocking has been highly influential in the formulation of modern learning theories. Some associative theories assume that learning is governed by an error-correcting rule that leads to stimuli being in competition for the control they acquire over behaviour. The predictive error can affect Pavlovian conditioning directly by altering the effectiveness of the US: A surprising or unexpected US is more effective than a fully predicted US. Accordingly, during compound conditioning with a pre-trained element A and a novel element B, primed activation of the US (via A) by reducing its processing would prevent the establishment of an associative link between B and the US (Rescorla and Wagner, 1972; Wagner, 1981). The predictive error can also have an indirect effect on Pavlovian conditioning: A stimulus which is a good predictor of an outcome (A) would command more attention than a novel stimulus (B). Focusing the limited processing power onto the stimulus with higher predictive value would

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prevent the association between B and the US (Mackintosh, 1975a; Pearce and Hall, 1980). In either case (poor processing of the US or poor processing of B) the B element would fail to acquire the properties of an effective conditioned stimulus, the outcome typically observed in the blocking experiments.

Other associative theories assume that during compound conditioning (AB+), associations of each element with the unconditioned stimulus will form independently (there is no acquisition deficit of B). The magnitude of the conditioned response (CR) to B would be determined by the retrieved memory of two competing cues, the comparator, A, and the target, B. At the time of test, the product of the association between the comparator and the target (A—B) and the association between the comparator and the US (A—US) would reduce excitation elicited by the target cue's direct association with the US (B—US). Therefore, according to this view, commonly known as the comparator theory, overshadowing and blocking are regarded as performance effects (e.g., Miller and Matzel, 1987; Stout and Miller, 2007).

A different approach to the cue competition effects assumes learning to depend upon the spatiotemporal distribution of events rather than upon the establishment of associations: The animal learns, for example, a temporal map – the times of onset and offset of the CS and the US – and uses this information in the decisions that determine their conditioned behaviour. If the expected time for the next presentation of the US in the presence of the A element is equal to the expected time for reward in the presence of the AB compound, then the individual will assign high predictive value – reinforcement rate – to A and low or null predictive value to the redundant B element (e.g., Balsam and Gallistel, 2009; Gallistel and Gibbon, 2000).

Other processes have been proposed that can account for cue competition effects by reference to a controlled rational-like process that helps the individual realize the redundancy of the target cue. These high-level processes of rational inference have been said to account for some instances of blocking in human predictive learning (e.g., De Houwer and Beckers, 2003; Lovibond, 2003; Mitchell and Lovibond, 2002) and some instances of forward blocking in the rat (e.g., Beckers et al., 2006; Blaisdell et al., 2006).

The heterogeneity of theories about blocking, and the fact that convincing evidence has been reported for all of them in experiments with vertebrates (mainly rats and humans) suggest that blocking is a complex multi-determined phenomenon. However, in spite of their differences, all these theories are able to predict the response deficit observed when testing the target CS, B, in the blocking procedures. One aspect they have in common is that the learning mechanisms they advocate would help the individual discount redundant information at the time of acquisition or test. These mechanisms would therefore play an important role in helping individuals optimally adapting their behaviour to the prevalent conditioning contingencies. It would be of interest to expand this rich theoretical analysis of causal learning to the invertebrate field.

As noted above, instances of Pavlovian conditioning have been reported in some invertebrate species: for example, in *annelids* (e.g., the earthworm *Lumbricus terrestris*, McManus and Wyers, 1979), *arthropods* (e.g., the honey bee *Apis mellifera*, von Frisch, 1953), *molluscs* (e.g., the snail *Helix pomatia*, Peschel et al., 1996; *Helix aspersa*, Ungless, 1998; the sea slug *Aplysia californica*, Hawkins et al., 1983; the slug *Lymax maximus*, Sahley et al., 1981a,b), and *platyhelminthes* (e.g., the planaria *Dugesia dorotocephala*, Thompson and McConnell, 1955; *Dugesia tigrina*, Prados et al., 2013). Compared to the rich vertebrate literature, there is a paucity of data in the invertebrate field, and little is known about the nature of the learning mechanisms that rule Pavlovian conditioning in invertebrates.

Some studies have attempted to relate the associative processes of invertebrates to those of vertebrates, paying special attention to the blocking effect, which has become a cornerstone for modern learning theory. Blocking has been observed, for example, in the *arthropod* honey bee (e.g., Couvillon et al., 1997; Smith and Cobey, 1994), in the *molluscs* garden snail (Acebes et al., 2009) and slug (Sahley et al., 1981a,b), and the *platyhelminth* planaria (Prados et al., 2013). In all of these experiments, the experimental group was always given pre-training with a cue A, followed by compound conditioning with AB and test trials with the added element B; that is the sequence A+, AB+, B (except Couvillon et al., 1997, which used a concurrent blocking procedure; see Table 1 for a summary of procedures and results). A deficit in the CR to the element B was observed in comparison with the standard control group given compound conditioning followed by test with one of the elements—AB+ B, a blocking effect.

However, the inequality of experience with A and the US (+) in the experimental and control groups described just above is troubling: Less response during the test with B in the blocking than in the standard control group could be due, for example, to habituation of the shock-US during the single conditioning phase (A+). This would lead to poorer conditioning of B during compound conditioning (AB+) rather than competition between the already predictive A and the new B elements. To account for this, control groups were added in some of the experiments in which the experience with the A element and the US was equated to the blocking group but in which the A element could not become a reliable signal of the US: random presentations of A and the US: A/+, AB+, B (Acebes et al., 2009; Smith and Cobey, 1994); and backward conditioning: +A, AB+, B (Sahley et al., 1981a,b; Smith and Cobey, 1994). The problem is that, in the two cases, the un-signalled presentations of the US could result in context conditioning, which would control part of the CR animals display during the final tests with the B element (the context is better protected from conditioning in the blocking group in which the US is signalled by the A element). To control for context conditioning, a third type of control was used in which a third element, C, was paired with the US in the first stage of the experiment: C+, AB+, B (Acebes et al., 2009; Smith and Cobey, 1994). However, this is hardly a satisfactory solution given that associative strength could generalize to B from C and A in the control group, and from A only in the blocking group, creating again an unbalanced design.

In the light of these considerations, some have pointed out that none of the control procedures used in the between-subjects designs, either alone or in combination, can provide univocal evidence of blocking; to avoid these problems the blocking and control treatments should be compared in a within-subjects design (Blaser et al., 2008).

Within-subjects designs, in which all the subjects are given the experimental and the control treatment, offer the ideal control for the influence that the inequality of experience with A and the US, context conditioning or generalisation could have in the magnitude of the response to the target cue B in the experimental groups of the between-subjects designs. Even the most thorough between-subjects demonstrations of blocking including several control groups, like the study by Smith and Cobey (1994) in which four control groups were used, are potentially exposed to criticism. Therefore, between-subjects designs with several control groups are not only expensive and laborious, but may also be inconclusive. Furthermore, usage of within-subjects designs would contribute to the reduction of the numbers of animals affected by experiments (following the 3Rs recommendations). In spite of these potential advantages, blocking within-subjects designs have been rarely used in the vertebrate learning literature (with exception of the literature on human predictive learning, e.g., Morís et al., 2012) and only once in the invertebrate literature (Blaser et al., 2008).

An early demonstration of the blocking effect using a within-subjects design was reported by Rescorla (1981); using pigeons and an autoshaping task, Rescorla gave differential reinforcement with