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The amount of exposure determines generalization in animal perceptual learning using short inter-stimulus intervals

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ABSTRACT

While human and animal perceptual learning (PL) had sometimes yielded similar results, there is evidence of some striking discrepancies. It has been proposed that such differences reflect the existence of multiple species-specific mechanisms, especially regarding to humans. However, it is also possible that those discrepancies are caused by procedural differences. One of the most important differences between PL experiments in humans and laboratory animals is the inter-stimulus interval (ISI) used. In the former, short ISI reliably produces PL, while in the latter reducing the ISI leads to paradoxical results. We report two experiments with rodents to prove that the length of exposure is a key element under such conditions. In the first experiment we replicated the paradoxical results already present in the literature using a short exposure. In a follow up experiment, we increased the exposure trials and obtained normal PL in animals using short ISI. Our results support current associative theories of PL and highlight the impact of procedural differences on this phenomenon.

1. Introduction

Research in perceptual learning has thrive since the pioneering work of Gibson (Gibson, 1963), with a significant boom from the early 2000's in the field of associative learning (for a recent review, see Mitchell and Hall, 2014). Numerous experiments have been conducted both in animals and humans, which have found some striking commonalities. One of such findings is the fact that the schedule of exposure to the stimuli affects posterior discrimination, that is, alternated exposure causes better discrimination than blocked – the so-called intermixed-blocked effect (I/B, Symonds and Hall, 1995). However, some critical differences were also found, which lead to the suggestion that specific mechanisms exists for different species (Mitchell and Hall, 2014).

The most relevant of these differences is related to the inter-stimulus intervals (ISI), as it has been found that using very short ISI produces a reliable I/B effect (that is, a superior discrimination after intermixed exposure) in humans, but not in animals. In human experiments the usual ISI is very brief (in the order of seconds, e.g. Lavis and Mitchell, 2006), or even zero (i.e. simultaneous exposure, Mundy et al., 2009), and all the exposure is given during the same day. Under such conditions, the usual result is a very robust I/B effect. This discrimination is often evaluated using same-different tasks on visual stimuli, with no conditioning involved. In contrast, in animal research the most common stimuli are flavours, with the usual ISI being of several hours and the exposure distributed throughout several days (Mackintosh et al., 1991; Symonds and Hall, 1995). Another procedural difference is the test itself, involving conditioning to one stimulus and measuring generalization to the other. While there are some examples of animal perceptual learning using short ISI (see, Bennett and Mackintosh, 1999; Honey and Bateson, 1996; Honey et al., 1994), the common finding is the shorter the ISI, worse is the discrimination, which in some instances can be even worse than following blocked exposure (Alonso and Hall, 1999; Rodríguez and Alonso, 2008).

This impairment of the I/B caused by shortening the ISI has been explained in terms of sensory preconditioning (Honey et al., 1994). If two stimuli are presented intermixed with a short interval between them (i.e. AX/BX/AX…) excitatory associations are likely to form between them as a result of temporal contiguity, in contrast with blocked exposure (AX/AX… BX/BX…). After conditioning one of them, such excitatory associations are expected to increase generalization of the conditioned response to the other. Why this same sensory preconditioning effect does not happen in human experiments could be explained by other procedural differences such as the differences in testing, as there should be no increase in generalization in a same-different task with no conditioning. Nonetheless, two experiments with humans have used flavours as stimuli and generalization testing with short ISI, and still have found the I/B effect (Dwyer et al., 2004; Mundy et al., 2006). Critically, Mundy et al. (2006) found that such effect was

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based on inhibitory associations being formed between the unique elements of the stimuli. This finding fits with the model proposed by McLaren and Mackintosh (2000), which anticipated that the formation of mutual inhibitory associations between the unique elements is responsible for the I/B effect.

In animals, there is also evidence that such inhibitory associations might be responsible for the I/B effect (e.g., Bennett et al., 1999). In an elegant series of experiments, J. Prados and A. Artigas demonstrated that this mechanism occurs preferentially with long periods of exposure, while with shorter periods other mechanisms (e.g. Hall, 2003) were responsible for the I/B effect (Artigas et al., 2006a, 2006b; Contel et al., 2011). While they used long ISI in their experiments, inhibitory associations are also expected to form when using short intervals (e.g., Wagner, 1981).

Thus, it is possible that a prolonged exposure leading to inhibitory associations between the unique elements A and B could reverse the effects of sensory preconditioning when using short ISI. To test this hypothesis, we conducted two experiments. In Experiment 1, rats received either intermixed or blocked exposure to two compound flavours for four days, followed by aversive conditioning to one of them and a generalization test on the other. We expect a diminished or abolished intermixed advantage explained by excitatory associations formed between the flavours, thus increasing generalization. In Experiment 2 we greatly increased exposure from four to twelve days, thus tripling the amount of training. In this case, we expect that the inhibitory associations overcome the sensory preconditioning, leading to a normal I/B effect such as that observed with short ISI in humans or with long ISI in animals.

2. Experiment 1

2.1. Method

2.1.1. Subjects and apparatus

The sample consisted of 16 Wistar rats with ad libitum mean weight of 517 g (range: 460–585 g). The animals had been used in a previously unrelated experiment, but were naïve to the procedures and apparatus of the present experiment. During the experiment, the rats were individually housed in translucent plastic cages measuring 35 × 22 × 18 cm, with wood shavings as bedding. They were maintained on a 12-h light/dark cycle (starting at 0800).

All of the flavoured solutions used were prepared with tap water on the day of each experimental session and were administered in the home cage using inverted 50 ml centrifuge tubes with stainless steel, ball-bearing-tipped spouts. Fluid consumption was calculated by weighing the tubes before and after the drinking sessions. For both experiments, AX and BX were 0.05% v/v caramel or hazelnut (counterbalanced) flavour solutions (Manuel Riesgo, Madrid) with a 9 g/l commercial sodium chloride solution. A distractor solution was added to the procedure, consisting of 20 g/l commercial sucrose. This procedure was used because the present experiments were part of a more extensive experimental series, and we had results using the same parameters, but it is not a relevant manipulation in the procedures detailed below. For conditioning, intraperitoneal injections of 0.15 M LiCl were administered at a volume of 1% of body weight.

2.1.2. Statistical analysis

We used General Linear Model analysis, adopting a rejection level of $p < 0.05$, and used Greenhouse-Geisser corrections when needed. Partial eta squared (η_p^2) and Cohen's *d* were used to report effect sizes.

2.1.3. Procedure

All the procedures explained here were approved by the Animal Research Ethics Committee (CEEA) from the University of Granada. Rats were divided into two groups (INT and BLK) with similar weights (means 514 g and 519 g, $t(14) = -0.28$, $p > 0.79$, $d = -0.13$). All rats were deprived by restricting the water availability to two daily sessions of 30 min at 1400 and 1900. Rats received three baseline days where water consumption was measured only during the morning session, since no relevant manipulations were conducted during the afternoon session. All groups consumed similar amounts of water during this period (last day means 11.43 ml and 10.64 ml, $t(14) = -1.27$, $p > 0.22$, $d = -0.64$).

Table 1
Design of Experiments 1 and 2.

	Group	Pre-exposure	Conditioning	Test
Experiment 1	INT_short	AX/W/BX_D and BX/W/AX_D	AX+	BX?
	BLK_short	AX/W/AX_D and BX/W/BX_D		
Experiment 2	INT_long	AX/W/BX/D and BX/W/AX/D	AX+	BX?
	BLK_long	AX/W/AX/D and BX/W/BX/D		

Note: A, B, D and X represent different flavours, W represents plain water. + refers to an i.p. injection of LiCl. The slash ("/") indicates rapid succession, the underscore ("_") indicates a separate session. *INT* and *BLK* refer to intermixed and blocked exposure respectively. The pre-exposure phase in Experiment 1 (*short*) was four days; in Experiment 2 (*long*) was twelve days.

The procedure is outlined in Table 1. The pre-exposure stage lasted four days (Days 1–4), where all rats received access to four solutions every day. During the first daily session at 1400, all rats received access to three different solutions. The INT group received 6 ml of solution AX for 10 min, followed by 4 ml of water for 5 min, and finally 6 ml of solution BX for 10 min. The order in which AX and BX were presented was alternated across days. The BLK groups had the same schedule, but they received presentations of AX during the first two days, with water in between, and BX during the last two days. Both groups received 5 min of the distractor on the second session at 1900, followed by 30 min of ad lib access to water to keep them hydrated. Thus, on the first day, rats in the INT group received the sequence AX-W-BX with D in the afternoon, while rats in the BLK group received AX-W-AX with D in the afternoon.

On the following 4 days (Days 5–8) rats received two conditioning trials (on Days 5 and 7) and two recovery days (on Days 6 and 8). On each conditioning trial rats had constant access to 10 ml of AX for 30 min, immediately followed by an i.p. injection of LiCl. On recovery days, rats had free access to water for 30 min at 1400. During the next three test days (Days 9–11), rats received ad lib access to BX for 30 min at 1400.

2.2. Results and discussion

Rats consumed virtually all of the fluid available during the pre-exposure sessions; and the mean consumption of AX decreased across the two conditioning trials in both groups: from 8.1 ml to 2.9 ml in group INT, and from 8.7 ml to 3.9 ml in group BLK. A repeated measures ANOVA conducted on these data, with Group and Trial as factors, confirmed a significant effect of Trial, $F(1, 14) = 33.83$, $p < 0.001$, $\eta_p^2 = 0.71$. No significant effect of group, $F(1, 14) = 1.38$, $p > 0.26$, $\eta_p^2 = 0.09$; or interaction, $F < 1$, were found. Fig. 1 (upper panel) shows consumption of BX across the three test days, and it indicates that the INT group generalizes the aversion more than the BLK group. A repeated measures ANOVA conducted on these data with Group and Trial as factors showed significant effects of Trial, $F(2, 28) = 3.75$, $p < 0.04$, $\eta_p^2 = 0.21$; and Group, $F(1, 14) = 7.20$, $p < 0.02$, $\eta_p^2 = 0.34$. No significant interaction was found, $F < 1$.

The results of Experiment 1 seem to indicate that, using short interstimulus intervals, intermixed exposure causes more generalization of the aversion from AX to BX. This is consistent with the idea that excitatory associations were formed between the compound flavours (Honey et al., 1994). This result is similar to previous studies that found worse discrimination after short ISI intermixed than after blocked exposure (Alonso and Hall, 1999; Rodríguez and Alonso, 2008). In the

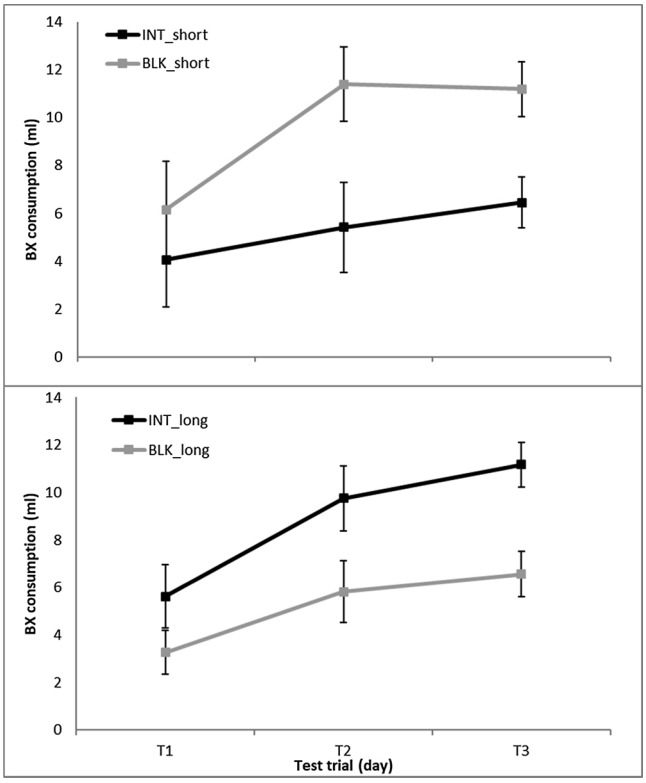

Fig. 1. Average consumption of BX solution during test. **Results of Experiment 1 and 2:** The figure represents average direct consumption (± SEM) of BX after pairing AX with an i.p. injection of LiCl. INT refers to the group that received intermixed exposure between AX and BX; BLK refers to the group that received blocked exposure. Water (W) was located in between presentations of the flavoured solutions. The **upper panel** depicts the results of Experiment 1, where both groups received *short* pre-exposure (4 days). The **lower panel** depicts the results of Experiment 2, where both groups received *long* pre-exposure (12 days).

next experiment we increased the amount of exposure rats received. If a prolonged exposure promotes the formation of inhibitory associations, then this reverse I/B effect should disappear, or, if such associations can overcome the sensory preconditioning, a full I/B effect could arise.

3. Experiment 2

3.1. Method

3.1.1. Subjects and apparatus

The sample consisted of a group of 16 naïve Wistar rats with ad libitum mean weight of 299 g (range: 276–325 g). All the remaining details are the same as in Experiment 1.

3.1.2. Procedure

Rats were divided into two groups (INT and BLK) with similar weights (means: 299 g and 300 g, $t(14) = 0.08$, $p > 0.94$, $d = 0.04$). All rats were deprived by restricting the water availability to two daily sessions of 30 min at 0930 and 1600. Both groups consumed similar amounts of water during baseline (last day means: 9.7 ml and 9.8 ml, $t(14) = -0.09$, $p > 0.93$, $d = -0.05$).

The general procedure is outlined in Table 1. It was essentially the same as in Experiment 1, but with some procedural changes. First, the four solutions were presented consecutively in the morning session, while in the afternoon all rats had ad lib access to water. Second, to ensure that all solutions were consumed, amounts presented were reduced to 5 ml of AX/BX or 3 ml of distractor or water. The critical manipulation was the increase of the pre-exposure from four to twelve days (Days 1–12). Because of the longer exposure more latent inhibition was expected, so we increased the amount of conditioning trials to three (Days 13, 15 and 17), with three rest sessions (Days 14, 16 and 18). Three test trials followed (Days 19–21). Every other detail not mentioned here was the same as in Experiment 1.

3.2. Results and discussion

Rats consumed almost all of the fluid available during the pre-exposure sessions. During conditioning, the mean consumption of AX decreased across the three conditioning trials in both groups: from 9.0 ml to 5.7 ml in group INT, and from 9.2 ml to 3.0 ml in group BLK. A repeated measures ANOVA conducted on these data, with Group and Trial as factors, showed a significant effect of Trial, $F(2, 28) = 42.15$, $p < 0.001$, $\eta_p^2 = 0.75$. No significant effect of Group, $F(1, 14) = 2.19$, $p > 0.16$, $\eta_p^2 = 0.14$; or interaction, $F(2, 28) = 4.04$, $p > 0.06$, $\eta_p^2 = 0.22$, were found[1] . Fig. 1 (lower panel) shows consumption of BX across the three test days in Experiment 2. It shows a typical I/B effect, where the INT group generalizes less than the BLK group from AX to BX. A repeated measures ANOVA conducted on these data with Group and Trial as factors showed significant effects of Trial, $F(2, 28) = 34.08$, $p < 0.001$, $\eta_p^2 = 0.71$; and Group, $F(1, 14) = 5.88$, $p < 0.03$, $\eta_p^2 = 0.30$. The interaction was not significant, $F(2, 28) = 2.13$, $p > 0.14$, $\eta_p^2 = 0.13$[2] .

The results contrast sharply with Experiment 1, where we found a reverse I/B effect. It seems that increasing the exposure counteracts the influence of excitatory connections. The idea that a long exposure allowed the formation of inhibitory associations would explain the current results, and is consistent with previous evidence (Artigas et al., 2006a; Bennett et al., 1999).

4. General discussion

In contrast with human experiments, where using a short ISI produces a normal I/B effect (Dwyer et al., 2004; Mundy et al., 2006), in animal studies trying to reduce the interval between successive stimuli seemed to yield negative or even paradoxical results in animals (Alonso and Hall, 1999; Bennett and Mackintosh, 1999; Honey and Bateson, 1996; Rodríguez and Alonso, 2008). A possible explanation for these results was based on sensory preconditioning: temporal contiguity would cause excitatory associations to form between the unique elements of the compound flavours, thus increasing generalization between them. Because results with humans seemed to suggest that inhibitory connections were responsible for the I/B effect when using short ISI and flavour stimuli (Mundy et al., 2006), and previous experiments with rats showed that such inhibitory links take longer to form (Artigas et al., 2006a, b; Artigas et al., 2006a; Contel et al., 2011), we decided to manipulate the length of pre-exposure in a procedure with short ISI.

Our results are consistent with this general idea. Experiment 1 shows that using a short ISI and short exposure causes a reverse I/B effect, where the intermixed group generalizes more between stimuli. This would be expected assuming that excitatory links are more likely to form in the intermixed condition. In this case, the short interval alternation ensured temporal proximity between the compound flavours, thus potentially allowing excitatory associations to form. Experiment 2

[1] Note: As the interaction approached significance, we run pairwise comparisons between groups for each day. No significant differences were found for any of the days, highest $t(14) = -1.90$, $p > 0.08$, $d = -0.95$. Overall the analyses do not support the existence of differences in conditioning, despite the high variability of the last day.

[2] Note: One tube of group BLK leaked on the first test day. Consumption for that rat was set at the group average for that trial for purposes of analysis and graphical representation. Completely removing that animal from analysis (resulting in n[BLK] = 7) did not change the overall results.

shows that increasing the length of pre-exposure suppresses the reverse I/B effect, and furthermore allows the expression of the normal I/B effect. This effect is presumably a result of the inhibitory associations outweighing the excitatory links formed in the early trials of the pre-exposure.

This idea is well accommodated within standard associative theory following Wagner (1981, see also, Brandon et al., 2003). This model proposes that presentation of a stimuli results in activation of its elements in a maximal processing state (A_1) during a relatively short time. The elements progressively decay to a state of marginal processing (A_2), and from there they slowly decay further to an inactive (I) state. Elements co-occurring in A_1 state will form excitatory associations, while inhibitory associations will be formed between elements in A_1 state and other elements in A_2. In our procedure, when the first stimulus is presented, its elements will be activated in A_1 state. By the onset of the second stimuli, some of them should have decayed to A_2. But because the ISI is short, it is likely that some of them remain in A_1. Thus, those A_1 elements of the first stimulus could form excitatory associations with the recently activated elements of the second stimulus. At the same time, inhibitory associations will be formed between the A_1 elements of the second stimulus and the A_2 elements of the first. If we assume that the proportion of A_2 elements is superior to the proportion of A_1 elements when the second stimulus appears, then the final net associative strength between both stimuli should be inhibitory. Then, why do we see a reverse I/B effect with short exposure? The model also proposes that the learning rate for excitation is higher than for inhibition. Thus, excitatory strength will grow rapidly, but will eventually be outpaced by the slowly increasing inhibitory strength.

This interpretation has some caveats that deserve further discussion. First, it can be argued that the different location of the distractor, and not the exposure length, is partially or totally responsible for the results. For instance, it is possible that a distractor placed immediately after the second stimulus could interfere with the formation of excitatory connections between both flavours, thus causing the lower generalization observed in Experiment 2. However, we have shown elsewhere (Recio et al., 2018) that the presence of this distractor after the presentation of the second compound, either at the end of the morning session (like in Experiment 2) or in the evening session (like in Experiment 1) produced equivalent results, not lending support to any interpretation based on differential dishabituation or excitatory associations between stimuli or between stimuli and distractor. Also, even if we assumed that the distractor in Experiment 2 somehow interfered with the consolidation of the excitatory associations, we would expect a null effect instead of less generalization after intermixed exposure. Thus, this procedural difference between experiments, although certainly inelegant, is not expected to affect the current results nor their interpretation. Second, and more substantial, is the issue that our interpretation relies on the formation of associations between both stimuli, excitatory with short exposure and inhibitory with long exposure. Direct evidence on excitatory associations between flavours is scarce, and it seems to require much shorter inter-stimulus intervals than the ones we have used in our experiments (see Lavin, 1976). In contrast, there is robust evidence of inhibitory associations between intermixed stimuli, although usually with longer inter-stimulus intervals (Artigas et al., 2006a; Espinet et al., 1995). Since we do not provide direct evidence of the formation of both types of associations, and our parameters are different from those present in the literature, our results are open to alternative explanations.

Artigas et al. (2012) propose a complete explanation also based on Wagner (1981), but resorting to salience modulation to explain the increased generalization with short exposure. In their paper, they argue that in a rapid exposure procedure, the presentation of the first compound would cause the common elements to be habituated (i.e. already activated in an A_2 state) when the second compound is presented. Thus, a higher proportion of the unique elements will be activated, increasing their processing and hence reducing their salience (by means of latent inhibition or long-term habituation). Note that the presence of a distractor in Experiment 2 is not expected to affect this process either, as the increased processing of the unique elements happens before it is presented. In contrast, with blocked exposure the relative interference of the common elements over the unique elements will be greater, because both will be habituated during the second stimulus presentation. This is expected to change as exposure proceeds, as the common elements are still presented twice as often as common elements overall (McLaren et al., 1989). However, the imbalance of processing should not be as big as in the intermixed case. This should cause a relatively higher salience of the unique elements after blocked exposure, interfering more with the association of the common elements with the outcome in the conditioning and with the expression of the conditioned response in the test. That is, the unique elements would be less salient after intermixed than blocked exposure, so the conditioned response would depend more on the common elements, increasing generalization. However, a longer exposure would neutralize this effect in at least two different ways. First, since it can be assumed that salience reduction follows a negatively accelerated curve, the salience imbalance between unique and common elements would tend to be more similar regardless of the exposure type. Second, as seen in Artigas et al. (2012) and explained above, inhibitory associations can explain why more extensive exposure could reverse the previously explained process. Artigas et al.'s salience modulation explanation has the advantage that it does not rely on excitatory associations between unique elements to explain the increase in generalization after short intermixed exposure, while still using mechanisms well predicted by associative theory.

To sum up, we showed that the worse discrimination found in animals when using short ISI can be reversed by increasing the amount of exposure to the stimuli. While our results do not allow us to draw any definitive theoretical conclusions, they are consistent with results in humans using similar procedures, and with previous results in animals using long ISI. We have outlined some possible mechanisms – the formation of excitatory-inhibitory associations or relative salience changes of the unique elements –, both compatible with current associative models (Wagner, 1981). Further research is needed to firmly establish the underlying mechanisms behind this effect.

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