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Effects of extended context discrimination training and context extinction on transfer of context dependency of conditioned flavor aversion

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ABSTRACT

We trained rats in a context discrimination paradigm by pairing a sucrose solution with lithium chloride in one context (conditioning context) and simple exposure to the same fluid in a second (neutral) context to establish a context-dependent aversion to the conditioned fluid. We then investigated whether transfer of the context dependency to a test fluid (a sodium chloride solution) was affected by two post-discrimination training treatments, an extended context discrimination training, and non-reinforced exposure to the conditioning context (context extinction). We found that the context-dependent flavor aversion that had been specific to sucrose transferred to the test fluid after the extensive training (Experiment 1). Context extinction eliminated the transfer effect that had been observed immediately after the context discrimination training (Experiment 2). In addition, an aversion acquired by sucrose through a simple conditioning of sucrose–LiCl pairings did not generalize to the test fluid (Experiment 3). These results emphasize the importance of a Pavlovian excitatory association between the conditioning context and nausea as a primary source of transfer of the context dependency, rather than a generalization of aversion acquired by the conditioned fluid to the test fluid.

1. Introduction

In Pavlovian conditioning paradigms, most acquisition and expression of conditioned responses come under the influence of the experimental context in which these responses have been conditioned (e.g., Bouton and King, 1983; Bouton and Swartzentruber, 1986; Hall and Honey, 1990). In studies employing a flavored, ingestible stimulus (such as food or a solution) as well as signaling where such stimulus is presented (Shishimi and Nakajima, 2007) or potentiating consumption of the stimulus (Petrovich et al., 2007), a conditioning context affects a preference for or aversion to the stimulus. For example, Archer et al. (1985) reported that an aversion to a saccharin solution, conditioned in a context by pairings of saccharin with an injection of lithium chloride (LiCl), did not appear in a distinct, test context (see also Bonardi et al., 1990; Leon et al., 2012). More recently, context discrimination training has been employed to investigate systematically the role of training contexts in which aversion is acquired to flavor stimulus. In context discrimination training, animals are given repeated pairings of a conditioned fluid with an LiCl injection in a conditioning context and simple exposures to the conditioned fluid in another (neutral) context. After establishment of the context discrimination, animals consume less of the conditioned fluid in the conditioning context than in the neutral context (e.g., Boakes et al., 1997; Ishii et al., 2006; Lopez and Cantora, 2003; Loy et al., 1993; Murphy and Skinner, 2005; Nakajima et al., 1995; Puente et al., 1988; Skinner et al., 1994).

Currently, there are two explanations for the context dependency of flavor aversion learning. First, the conditioning context–nausea association account argues that during discrimination training, not only a conditioned fluid but also a conditioning context is associated with nausea via an excitatory link. According to this account, when the conditioned fluid is presented in the conditioning context at testing (after discrimination training), an aversion to the conditioned fluid is observed because of the combination of the associative strengths acquired by the conditioned fluid and conditioning context (Loy et al., 1993). Employing a blocking design, Lopez and Cantora (2003) demonstrated the associative strength acquired by a conditioning context. They first established a context-dependent sucrose aversion in rats through context discrimination training; animals then received a flavor

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aversion conditioning with a sodium chloride (NaCl) solution. Half of the animals (the blocking group) received this second conditioning in the original conditioning context, whereas the remaining animals (the control group) received the conditioning in the original neutral context. They found that the animals in the blocking group acquired a weaker NaCl aversion than those in the control group, suggesting that the conditioning context acquired a substantial associative strength with nausea during the discrimination training, and this association blocked acquisition of the conditioned aversion to NaCl (see also Kwok and Boakes, 2012; Symonds and Hall, 1997; Symonds et al., 1998; Willner, 1978).

The second explanation for the context dependency of a flavor aversion is that a conditioning context is not established as a conditioned excitor; rather, it acquires the function of occasion setting. According to the occasion setter account, a conditioning context positively modulates an association between a conditioned fluid and nausea by reducing the threshold for a representational activation of nausea, or by associating hierarchically with the conditioned fluid–nausea association (Boakes et al., 1997; Murphy and Skinner, 2005). Loy and Lopez (1999) demonstrated the validity of this explanation by establishing a biconditional context discrimination in rats. Animals received both repeated pairings of a vinegar solution with LiCl and simple exposures to a coffee solution in a context (Context A). After demonstrating a differentiated consumption between the two solutions in Context A, the role of two solutions was reversed in a second context (Context B); that is, animals received both coffee–LiCl pairings and simple exposures to vinegar in Context B. After the successive discrimination training, Loy and Lopez (1999) found specific suppressions in consumption of vinegar in Context A, and in consumption of coffee in Context B (for similar findings in conditioned flavor preference studies, see Dwyer and Quirk, 2008; Gonzalez et al., 2012). In the biconditional discrimination, each of the contexts in itself cannot signal reinforcement or non-reinforcement of the flavor stimuli; it is therefore difficult to explain the established context-dependent behavior in terms of simple excitatory associations acquired by the training contexts (cf. Brandon and Wagner, 1998; Pearce, 2002).

To test the distinct predictions made by the two accounts, the effect of non-reinforced exposures to a conditioning context after establishing a context-dependent flavor aversion and transfer of the context dependency have been evaluated. For example, some studies demonstrated that a context dependency of a flavor aversion disappeared (Loy et al., 1993; Skinner et al., 1994) or attenuated (Nakajima et al., 1995) following exposures to the conditioning context without reinforcement but with drinking water that differs from the conditioned fluid. According to the conditioning context–nausea account, this "context extinction" is expected to reduce an excitatory associative strength between the conditioning context and nausea (or produce a new inhibitory link antagonistic to the excitatory association). Because the context-dependent aversion is partly supported by the excitatory association acquired by the conditioning context, the contextual control of aversion should decrease when the association is weakened. In contrast, the occasion setter account predicts that a context-dependent aversion should be intact even after context extinction. This is because it has been widely recognized that post-conditioning non-reinforced exposures to a stimulus do not attenuate its established role of occasion setting (e.g., Holland, 1989, 1992; Rescorla, 1986; Swartzentruber, 1995).

Interestingly, Murphy and Skinner (2005) succeeded in both the disruption of a context-dependent aversion by a context extinction with a water presentation and showing failure of the context extinction effect by a context extinction without the water presentation (see also Nakajima et al., 1995; Skinner et al., 1994). The authors argued that the role of a conditioning context as an occasion setter could be diminished only by the context extinction in the presence of an appropriate target of the occasion setter, in this case, drinking response, and concluded that their results were in favor of the occasion setter account. The validity of this explanation should be further tested in future studies. However, it is important to note that the associative property of conditioning context acquired during context discrimination training remains elusive because of the multiple effects of context extinction.

The second effect on which the two accounts have made distinct predictions is transfer of a context dependency of aversion to a second, untrained test fluid, which is examined in the present study. The occasion setter account cannot successfully predict transfer to test fluid, i.e., that trained animals would consume less of a test fluid in the conditioning context than in the neutral context. This is because, according to the account, a modulation function acquired by the conditioning context is usually specific to the conditioned fluid (e.g., Bonardi, 1989; Holland, 1983). In contrast, the context–nausea association account assumes that the associative strength acquired by the conditioning context is a key factor of context-dependent aversion; this account thus allows for successful prediction of transfer based on summation of the associative strengths acquired by the conditioning context and the strength of associations generalized from the conditioned fluid to the test fluid. However, the results of previous studies are mixed because they have reported both successful transfer (Boakes et al., 1997; Ishii et al., 2006; Loy et al., 1993) and failed transfer (Puente et al., 1988).

However, in the first place, whether the successful transfer is evident cannot by itself elucidate the associative property of a conditioning context (cf. Lopez and Cantora, 2003; Symonds and Hall, 1997; Symonds et al., 1998). Indeed, either hypothesis can explain both success and failure of transfer by post hoc assumptions regarding the degree of generalization from conditioned fluid to test fluid. The conditioning context–nausea association account typically predicts a success of transfer rather than a failure. However, if the stimulus generalization is weak, an available associative strength should not reach the threshold for suppression of consumption when the test fluid is presented in the conditioning context, resulting in a failure of transfer. In contrast, the occasion setter account usually predicts a failure of transfer rather than a success. However, if the stimulus generalization between the conditioned and test fluids is strong, the conditioning context should exert its modulation ability on the test fluid, resulting in a successful transfer (Bonardi and Ward-Robinson, 2001).

At present, as is the case with context extinction, only limited conclusions can be drawn directly from success and failure of transfer in clarifying the acquired function of a conditioning context. This difficulty might be attributable in part to lack of knowledge about the factors influencing success and failure of transfer. Therefore, in the present study, we sought to reveal the basic characteristics of transfer by examining the effects of extensive discrimination training (Experiment 1) and context extinction (Experiment 2): according to the context–nausea association account, the two treatments were expected to affect success and failure of transfer, as explained in detail below. However, a stimulus generalization between a conditioned fluid and a test fluid would confound the transfer effect. In our experiments investigating the effects of post-context discrimination treatments, we employed the fluids between which the stimulus generalization would be unexpected: they are a sucrose solution as conditioned fluid and an NaCl solution as test fluid. Although such generalization has not been found in our laboratory, some authors have pointed out the difficulty in excluding this stimulus generalization effects completely from interpreting data (Lopez and Cantora, 2003; Symonds and Hall, 1997; Symonds et al., 1998). Consequently, we conducted an additional experiment (Experiment 3) to test whether an aversion to the conditioned fluid