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Effect of water temperature on swimming-based taste aversion learning in rats

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ABSTRACT

Swimming endows rats with conditioned aversion to a taste solution consumed shortly prior to swimming. The present study explores the effects of water temperature on this swimming-based taste aversion learning using simple conditioning (Experiment 1) and differential conditioning (Experiment 2) paradigms. In both experiments, swimming in 22 °C water effectively established taste aversion, while the aversion based on swimming in 30 or 38 °C water was weak and ambiguous. These findings are in contrast with the hypothesis that the energy expended during swimming is a crucial factor in the establishment of this learning, because it is known that the amount of physical activity is higher in warmer water.

1. Introduction

Nakajima and Masaki (2004) reported that confinement of rats in water containers (hereafter "pools") establishes a weak but statistically reliable aversion to taste solutions consumed shortly prior to the confinement. We have conducted a series of experiments since then designed to gain deeper insights into this learning phenomenon. First, we have shown that pairing of taste and confinement is necessary to trigger this phenomenon (Nakajima & Masaki, 2004; Masaki & Nakajima, 2004a, 2004b), implying that it is a form of Pavlovian conditioning, with taste as a conditioned stimulus (CS) and pool confinement as an unconditioned stimulus (US). Second, swimming activity is an essential US component for this conditioned taste aversion (CTA), as being wet alone is not effective in establishing CTA in rats; moreover, water levels (i.e., the necessity of swimming) determine the degree of CTA (Masaki & Nakajima, 2005). Thus, hereafter we designate this particular CTA as "swimming-based CTA" in rats. Third, the degree of swimming-based CTA is a positive function of the length of time (duration) that rats are confined to pools (Masaki & Nakajima, 2005, 2006). Fourth, swimming-based CTA is establishable with a 30-min delay between CS and US (Masaki & Nakajima, 2004b). Fifth, simultaneous conditioning procedures (swimming in flavored water) yields only a very weak CTA (Nakajima, 2015). Finally, previous swimming experience strongly alleviates swimming-based CTA (US pre-exposure effect: Masaki & Nakajima, 2004a, 2010). Notably, US post-exposure is also effective, although the effect is smaller than the US pre-exposure effect (Masaki & Nakajima, 2010).

Despite these studies on swimming-based CTA, a possibly important factor that remained to be investigated was the influence of water temperature. In all aforementioned studies, the water was at room temperature of 22 °C for convenience. Water temperature, however, may have significant effects on the activity levels of the confined rats. For example, Bruner and Vargas (1994), who monitored the activity of rats in relatively large square pools (40 cm × 40 cm at the water surface) filled with water of temperatures varying from 14 to 47 °C between the groups of rats, found that the rats' activity is a V-shaped function of water temperature, with the lowest levels of activity exhibited by rats in pools filled with 23 °C water. Notably, Baker and Horvath (1964), using a mid-sized cylindrical pool (27 cm in diameter at the water surface), reported that rats swam for longer periods of time, suggesting higher

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activity, in 37 °C water than did rats in water with temperatures of 19 or 42 °C.

It is worth mentioning here that initial demonstrations of swimming-based CTA derived from the hypothesis that physical activity generates CTA through energy expenditure (Nakajima & Masaki, 2004), because swimming is highly exhaustive (Benthem et al., 1994). The energy-expenditure hypothesis was originally proposed by Nakajima, Hayashi, and Kato (2000) as an explanation for running-based CTA, which was first reported by Lett and Grant (1996) and has since been examined by numerous researchers (see Boakes & Nakajima, 2009, for a review). Two studies have subsequently questioned the validity of the hypothesis concerning running-based CTA, however; for one, supplementation of energy supply (calories from sugar), which should compensate for the energy expended by running, did not alleviate running-based CTA (Nakajima, 2011), and second, conspecific fighting, which is also a highly energy-draining activity, was not an effective US for establishing CTA (Nakajima, Kumazawa, Ieki, & Hashimoto, 2012). Although these results suggest that energy expenditure is neither a necessary nor sufficient condition for establishing running-based CTA, they do not invalidate the claim that *swimming*-based CTA results from energy expenditure.

The primary objective of the current study is a pragmatic one: to find a proper water temperature for establishing swimming-based CTA in rats. Notably, the body temperature of rats (at a room temperature of 22 °C) is 37–38 °C (Gudjonsson, 1932). Thus, the three water temperatures employed in this study were at room temperature (22 °C), at the body temperature of rats (38 °C), and halfway in between the two (30 °C). Because water temperature affects the activity level of rats in water, the secondary goal of this research is to test the validity of the energy-expenditure hypothesis for swimming-based CTA. This hypothesis predicts that the amount of swimming-based CTA should be a positive function of water temperature, because within this range of temperature (22–38 °C), the activity of rats is expected to be linear (Baker & Horvath, 1964; Bruner & Vargas, 1994).

In the current study, Experiment 1 attempts to endow rats with swimming-based CTA by a simple conditioning procedure. Effect of water temperature on the CTA is to be evaluated by between-group comparisons. The generality of the finding of Experiment 1 is assessed in Experiment 2 with a differential conditioning paradigm.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

The subjects were 32 experimentally naïve male Wistar rats (Slc:Wistar/ST) purchased from a local supplier (Japan SLC, Inc., Shizuoka, Japan) 6 days before the experiment. The animals were housed in individual, hanging home cages in a vivarium and kept on a 16:8 h light–dark cycle (lights on at 0800 h) under conditions of 22 °C and 55% humidity. Rats were maintained on an ad-lib food schedule in the home cages, but water access was restricted to 15 min each day (1000–1015 or 1100–1115 h, see below). Tap water was accessible from a metal nozzle protruding through a hole in the center of the back wall of each cage. On the first experimental day, the rats were 9 weeks old, and their mean weight was 268.6 g (range: 257–286 g).

2.1.2. Apparatus

The rats were transferred in individual compartments in a carrying cart to a conventionally illuminated experimental room containing 16 drinking cages on a table and 12 pools on the floor. The travelling time from the vivarium to the experimental room was around 1 min. The drinking cages were copies of their home cages, which were made of wire with two solid metal side walls ($20 \times 25 \times 18.7$ cm, w × l × h). Tap water or sweetened water (0.2% sodium saccharin in tap water) at room temperature (22 °C) was provided via a glass bottle with a metal spout inserted from the cage ceiling; the end of the spout was 16.5 cm above the cage floor. Bottles were separated by 8 cm when two were used simultaneously in a choice test.

The pools consisted of plastic garbage containers (40 cm in diameter at the water surface) filled to a height of 30 cm with 32 L of tap water the day before each swimming day. Water temperatures were raised to around 30 °C in four pools and around 38 °C in an another set of four pools via electric heaters (SunArt SCH-901, Kumagai Electric Works, Osaka, Japan) immediately prior to each swimming session. No temperature controls were administered for the remaining four pools; thus, water temperatures remained at room temperature (22 °C). Water was replaced in all of the pools at the end of each day.

2.1.3. General protocol

Laboratory assistants, who were not informed of the hypothesis underlying the research, administered the experimental protocols. The rats were assigned to one of two squads ($n = 16$ each) consisting of four rats each from four treatment groups (Groups 22 °C, 30 °C, 38 °C, and No-Swim). On each day, the first and second squads of rats were moved to the experimental room for treatment sessions at 1400 and 1500 h, respectively. Four hours before each session (i.e., 1000 h for the first squad and 1100 h for the second), the rats were given access to tap water in the home cages for 15 min. This was to keep the water-deprivation levels of the four treatment groups equal. This pre-session watering was also intended to reduce thirst of rats, in order to facilitate detection of weakly conditioned taste aversion.

2.1.4. Adaptation, conditioning, and testing

On Days 1–3, all rats were adapted to drinking tap water in the drinking cages for 15 min. On Days 4–6, they were given access to saccharin solution for 15 min, then immediately immersed for 20 min in a 22 °C, 30 °C, or 38 °C pool, or confined to the individual compartments of the cart for 20 min (i.e., No Swim treatment). All rats assigned to the three swimming treatments were lightly dried with towels before being returned to the cart, and then, along with the No Swim rats, carried back to the vivarium.