International Journal of Comparative Psychology, 2009, 22, 141-152.

Incentive Relativity and the Specificity of Reward Expectations in Honey Bees

Daniel D. Wiegmann
Bowling Green State University, U. S. A.

Brian H. Smith
Arizona State University, U. S. A.

Honey bees were trained in a proboscis extension response procedure on a high quality reward to one of two odors under one of two contexts and then on a lower quality reward under the alternative context to the alternative odor. The performance decrement induced by the reduced reward, revealed by comparisons with subjects trained continually on the lower reward, was independent of odor-context combinations or the order of experience with stimuli. In a second experiment subjects were forward or backward conditioned to a high quality reward or fed unconditionally and then trained on a low reward in a novel context to a novel odor. The observed performance decrement depended only on exposure to the high quality reward. These results suggest that incentive contrast effects arise from a simple mechanism—the comparison of a current incentive with experienced incentives—that is effectively independent of cues that signal a reward.

Crespi (1942, 1944) discovered that rats anticipate the magnitude of a reward when they are trained to run down a runway to a goal box that contains a food reward (Elliott, 1928; Zeaman, 1949). In particular, he observed that rats trained on a high reward run more slowly to the goal box if the magnitude of the reward is suddenly reduced and, importantly, that these subjects temporarily run *more slowly* to the goal box than subjects in a control group that are trained continually on the lower reward. This observation was of special importance because it appeared to contradict the postulate that incentive determines the rate at which a stimulus and a response become associated (Hergenhahn & Olson, 2001; Hull, 1943, 1952). The numerous *incentive relativity* studies inspired by this discovery revealed that many animals form reward expectations (Flaherty, 1996). Indeed, an incentive contrast effect was observed in honey bees more than three decades ago and later studies implicated, as in vertebrates, a frustration-like process induced by the reduction of a reward (Bitterman, 1976; Couvillon & Bitterman, 1980, 1984; Shinoda & Bitterman, 1987).

Incentive relativity studies on vertebrates suggest that multiple mechanisms underlie responses to shifts of a reward (Flaherty, 1996; Mackintosh, 1974; Williams, 1983). The magnitude of incentive contrast effects in these studies (i.e., the responses of subjects that experience a reward shift relative to the responses of subjects that experience the secondary reward continually, but are otherwise treated identically) reveals that reward expectations are under direct

This research was conducted while D. D. Wiegmann was on faculty improvement leave and he thanks Bowling Green State University for financial support and the School of Life Sciences, Arizona State University for their hospitality. J. Latshaw provided technical support and advice on experimental procedures. The authors thank H. C. Cromwell, M. R. Papini and two anonymous reviewers for helpful comments on an earlier draft of this paper. Correspondence concerning this article should be addressed to D. D. Wiegmann, Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403, U. S. A. (ddwiegm@bgsu.edu).

stimulus control. In simultaneous incentive contrast experiments, where two stimuli with different schedules of reinforcement are presented alternately, the behavioral contrast that results from the transition of reinforcement schedules is more pronounced, for example, when the reinforced stimuli share many common elements (Bloomfield, 1972; Blough, 1988; Bower, 1961; Chechile & Fowler, 1973). In addition, static contextual cues—the apparatus and other background cues—may contribute to contrast effects induced by a reduction of reward (Dachowski & Brazier, 1991; Daniel, Wood, Pellegrini, Norris, & Papini, 2008; Flaherty, 1982). For example, rats trained alternately in low and high reward runways located in different rooms run more slowly to the goal box in the former runway than subjects trained on a low reward in both runways (Flaherty & Avdzej, 1976; Flaherty, Blitzer, & Collier, 1978).

Incentive contrast studies with honey bees and bumble bees similarly suggest that conditioned and static contextual stimuli are involved in the formation of reward expectations. The control of reward expectations by conditioned stimuli is evident in a study in which honey bee foragers were trained alternately to a stimulus A that contained a 50% sucrose solution reward and a stimulus B that contained a 20% sucrose solution reward and then tested a few minutes after a final exposure to B to either A or B under conditions in which both stimuli contained the low reward (Couvillon & Bitterman, 1984). In particular, subjects tested to A showed a significant disruption of consummatory behavior relative to subjects tested to B. The control of reward expectations by static contextual stimuli is implicated in studies of honey bee and bumble bee choice behavior (Greggers & Mauelshagen, 1997; Greggers & Menzel, 1993; Menzel, 2001; Waldron, Wiegmann, & Wiegmann, 2005; Wiegmann, Wiegmann, & Waldron, 2003). For example, bumble bee foragers trained to a high reward stimulus are likely to sample a novel stimulus that contains a low quality reward if the reward contained in the familiar stimulus is reduced, but subjects temporarily fail to consume the identical, low quality reward contained in *either* stimulus (Waldron et al., 2005; Wiegmann et al., 2003).

In vertebrates behavioral responses induced by reward shifts also appear to be modulated by mechanisms that are effectively independent of stimuli that signal a reward. Incentive contrast effects in rats occur, for example, even when a radical contextual shift is coincident with a reward reduction (Flaherty, Hrabinski, & Grigson, 1990; Grigson, Spector, & Norgren, 1993). These results reveal behavioral responses that do not depend on associatively reactivated expectancies, or *cued-recall relativity*, and implicate *recognition relativity*, incentive contrast effects that arise from the ability of a subject to recognize a difference of the magnitude of incentives (Papini & Pellegrini, 2006; Daniel et al., 2008).

In this study we conducted two experiments in which we manipulated conditioned stimuli and the context of reinforcement to minimize the influence of cued-recall memory on the responses of restrained honey bees to a reduction of reward. The results of these experiments suggest that experience with food is sufficient to instantiate reward expectations and that incentive contrast effects in

honey bees, like vertebrates, are modulated by mechanisms that are effectively independent of cues that signal a reward.

Experiment 1

In a standard successive negative incentive contrast design subjects are trained first on a high reward and later under identical conditions on a lower reward. The behavior of these subjects is compared to the behavior of subjects trained continually on the lower reward. The design of this experiment involved the addition of a concomitant shift of conditioned and contextual stimuli with the reduction of reward.

In this experiment, subjects were trained in a proboscis extension response (PER) procedure in two sessions to an odor stimulus in an illuminated arena. In the initial session subjects were trained on a high or low quality reward to one of two odor stimuli under one of two light backgrounds. In the second session all subjects were trained on a low quality reward to the alternative odor under the alternative light background. Afterward, subjects were tested without reinforcement under conditions of the first and second sessions to ensure that any difference of performance in the second session between subjects that experienced a reward reduction and subjects trained continually on a low quality reward could not be attributed to satiety.

Method

Subjects

Honey bees (*Apis mellifera*) were collected individually into small glass containers when they exited from outdoor colonies maintained at Arizona State University. Individuals were cooled until they became motionless and they were then secured in a plastic harness in manner that allowed them to move their antennae and mouthparts. Bitterman, Menzel, Fietz, & Schäfer (1983) describe this procedure in detail. Subjects were allowed to acclimate undisturbed for 2-3 h and they were then tested for their responsiveness to sucrose by antennal stimulation with a 2-µl droplet of 10% (weight percent) sucrose solution. Individuals were excluded from the study if this stimulation failed to elicit proboscis extension. In this responsiveness test prospective subjects were not allowed to consume the sucrose solution.

Apparatus

Individuals were PER conditoned in a 15 x 15 x 15 cm black acrylic arena lined on the top, bottom and sides with textured aluminum foil, which reflected light produced by two light-emitting diodes (Unitech Systems Inc., Part No. N500TBG4D) mounted on the rear floor of the arena. The two diodes emitted blue (464-475nm) or green (520-535nm) light with an intensity of 3200 mcd. The light conditions under which individuals were trained in this experiment are known to modulate the strength of learned olfactory associations (Gerber & Smith, 1998).

The front of the arena was open and subjects were placed in the center of the arena when they were trained. A 1 ml glass syringe—plunger removed—that contained a 35 x 2.5 mm piece of filter paper laden with 3 µl of pure 1-hexanol ($CH_3(CH_2)_5OH$) or geraniol ($C_{10}H_{18}O$) was positioned on a stand in front of the arena to deliver odors to subjects. A programmable logic controller was activated a few seconds after a subject was placed into the arena. The controller regulated a valve that shunted air through the syringe and it triggered a tone to signal the appropriate time to deliver a

reward. An exhaust duct located in the back wall of the apparatus vented odors from the arena. The room was illuminated by a 25-W red light, not easily detected by honey bees (Winston, 1987).

Procedure

Subjects were classically conditioned to either 1-hexanol (X) or geraniol (R) under blue (B) or green (G) background illumination in two sessions, each of which consisted of five trials. In the first session of the experiment the reward was a 2-µl droplet of either 10% (+) or 40% (++) sucrose solution. A trial was initiated with the placement of a subject into the arena. In each trial the odor stimulus was delivered to a subject for 4 s and a reward was delivered 3 s after the start of odor delivery. The trials within a session were separated by 5 min and 10 min separated the last trial of the first session and the first trial of the second session.

All four light and odor combinations were used in the first session in different treatment groups. Half of all subjects exposed to each light and odor combination were rewarded consistently with the low (XB+, XG+, RB+, RG+) or high (XB++, XG++, RB++, RG++) sucrose solution reward. In the second session of the experiment subjects were trained to the alternative odor under the alternative light condition on a 2-µl droplet of 10% (+) sucrose solution reward. This design yields a total eight groups, four odor and light combinations, subdivided into groups trained on a low or high reward. Ten subjects were assigned randomly to each of the treatments.

Each subject was tested 5 min after the final trial of the second session, first under the light and odor conditions used in the initial session of the experiment and then, 5 min later, under the light and odor context experienced in the second session to ensure that any decrement of performance observed in the second session by subjects who experienced a reward reduction could not be attributed to a lack of motivation to feed. Subjects were not rewarded in either of the tests. The experimental design is summarized in Table 1.

Table 1
Summary of the Design of Experiment 1.

Session		Test	
1	2	1	2
XB++	RG+	XB	RG
XB+	RG+	XB	RG
XG++	RB+	XG	RB
XG+	RB+	XG	RB
RB++	XG+	RB	XG
RB+	XG+	RB	XG
RG++	XB+	RG	XB
RG+	XB+	RG	XB

Note: In Experiment 1 subjects were trained to either 1-hexanol (X) or geraniol (R) under blue (B) or green (G) background illumination. The symbols + and ++ identify reinforcement with a low and high reward, respectively. In tests subjects were not rewarded (indicated by a lack of a + or ++). Incentive contrast effects are revealed by comparisons of the behavior of subjects that experienced different reward levels in the first session and identical odor and light conditions in each session. These respective treatment and control groups are listed in pairs.

Statistical Analyses

In each trial and in the two tests the response of a subject was scored as a one or a zero if a subject did or did not extend its proboscis within 3 s of the initiation of odor delivery, respectively; that is, a positive response was scored only if proboscis extension occurred before the controller

triggered the tone that signaled reward delivery. The proportion of trials in which a subject extended its proboscis was recorded for each session and a repeated measures analysis of variance, with post-hoc *t* tests, was used to compare the performance of subjects over the two sessions, with the light and odor reinforcement history in the initial session as factors. The independence of the performance of subjects in the unrewarded tests and their reinforcement history in the first session was evaluated with a Fisher's exact test (Sokal & Rohlf, 1995).

Results

Figure 1 shows the acquisition curves for the two sessions. These curves reveal that subjects trained on a high quality reward in the first session of the experiment responded poorly in the second session relative to subjects trained in the initial session on a low quality reward. The repeated measures analysis of variance yielded a significant main effect for the experimental session ($F(1, 72)= 14.24$, $p = 0.0003$) and a significant interaction between sessions and the level of reinforcement experienced by subjects in the first session ($F(1, 72) = 36.45$, $p < 0.0001$). The analysis indicates that subjects trained on a high quality reward responded significantly more often to the odor stimulus than subjects trained to the lower quality reward in the first session (Figure 1; $t(72) = 2.50$, $p = 0.0146$). But subjects trained on a high quality reward in the first session performed less well in the second session than did subjects rewarded with a low concentration sucrose solution in the first session ($t(72) = -6.59$, $p < 0.0001$). No other main effects or two-way or higher-order interactions were significant. The low level of responses by all subjects in the first trial of the second session also implies that subjects perceived the light-odor stimulus compounds experienced in the two sessions as distinct from one another.

In the initial test 34 of the 40 subjects that experienced a reward reduction and 30 of the 40 subjects that were trained continually on the low quality reward responded to the odor and light conditions under which they were initially trained. These response frequencies do not differ significantly (Figure 1; Fisher's exact test, $p = 0.4024$). But only 16 of the former subjects responded in the second test—under the odor and light conditions of the second session—in comparison to 32 of the subjects trained continually on the low quality reward (Fisher's exact test, $p = 0.0005$). These tests confirm that the decrement of performance in the second session by subjects who experienced a reduced reward was not due to satiety.

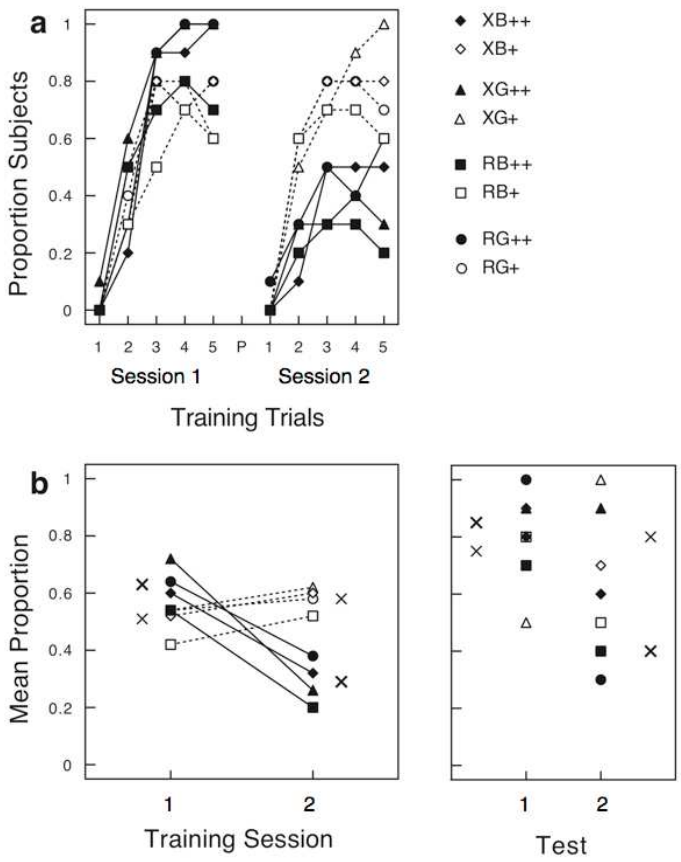

Figure 1. Acquisition curves and test responses of subjects in Experiment 1 reveal a contrast effect as a result of the reward reduction between sessions. (**a)** Proportion of subjects that responded with proboscis extension to odor delivery in each trial of the first and second sessions. The intersession inteveral is indicated by P. (**b)** Mean response rate for subjects in each session. Overall means for subjects trained initially on a high (++) or low (+) reward are indicated by the symbols **x** and x, respectively. Table 1 identifies legend symbols, which correspond to the stimuli and reward experienced by subjects in the first session.

Experiment 2

In this experiment our objective was to determine whether experience with food is sufficient to instantiate reward expectations. This experiment also involved two sessions, with subjects divided into three groups. The results of the Experiment 1 revealed that neither the combination of the olfactory stimulus and background illumination used to train subjects in the first session nor the order in which subjects were trained on particular light-odor stimulus compounds had an effect on the magnitude of the observed incentive contrast effect and for this experiment one odor-light treatment used in Experiment 1 was arbitrarily chosen to train subjects in two of the three groups. In particular, subjects in one of these

groups were forward conditioned on a high or low quality reward to geraniol under green background illumination and subjects in a second group were backward conditioned to these stimuli. Subjects in the third group were simply fed a high or low concentration of sucrose solution outside the arena. In the second session all subjects were trained to 1-hexanol under blue background illumination on a low quality reward.

An unrewarded test of the responsiveness of subjects was conducted after completion of the second session to ensure that any reduced performance in the second session by subjects that experienced a high sucrose solution concentration in the first session could not be attributed to satiety. In this test a lack of motivation to feed would be evident in a low level of responses by subjects forward conditioned on a high quality reward in the first session, relative to the performance of subjects forward conditioned initially on a low quality reward.

Method

Subjects

Individuals were collected, harnessed and tested for their responsiveness to sucrose solution as described in Experiment 1.

Apparatus

The apparatus used in this experiment was the same apparatus used in Experiment 1.

Procedure

Subjects were divided randomly into three groups. In the first session subjects in one group were PER conditoned on RG+ or RG++ as described for the first session of Experiment 1. Subjects in a second group were backward conditioned to these stimuli. These subjects were fed a 2-µl droplet of 10% or 40% sucrose solution in the dark, outside the arena and then placed immediately into the arena, where they were treated like subjects in the former group, except that no sucrose reward was delivered (+RG, ++RG). Subjects in a third group were simply fed a 2-µl droplet of 10% or 40% sucrose solution in the dark, outside the arena once every 5 min (+, ++). In the second session of the experiment all subjects were trained, as described in Experiment 1, in 10 trials on XB+. The final trial of the first session and the first trial of the second session were, as in Experiment 1, separated by 10 min. This design yields a total six treatments and 20 subjects were assigned to each of the treatments.

The responsiveness of each subject to geraniol under green light was tested after the second session to ensure that any decrement of performance observed in the second session by subjects fed or rewarded with a high concentration of sucrose solution in the first session could not be attributed to satiety. The interval between the final trial of the second session and the test for each subject was 5 min and in the test subjects were not rewarded. The experiment is summarized in Table 2.

Statistical Analyses

In the first session the responses of subjects that were backward or forward conditioned were scored as a one or a zero if proboscis extension did or did not occur within 3 s of the initiation of odor delivery, respectively. (In the first session subjects fed unconditionally were neither exposed to olfactory nor visual stimuli and, hence, these subjects have no scored responses). Individual responses were scored in each trial of the second session and in the test for all subjects. An analysis of variance was used to compare the performance of subjects in the first session, where the order of reward and stimuli delivery and the quality of reward served as factors. The 10 trials of the second session were divided into two equal blocks of five trials and a repeated measures analysis of variance

was used to compare the performance of subjects over the second session, with light and odor exposure and reinforcement history as factors. The independence of performance in the test and experience with stimuli and reinforcement history of subjects in the first session was evaluated with a Fisher's exact test (Sokal & Rohlf, 1995).

Table 2
Summary of the Design of Experiment 2.

Session		Test
1	2	
RG++	XB+	RG
RG+	XB+	RG
++RG	XB+	RG
+RG	XB+	RG
++	XB+	RG
+	XB+	RG

Note: Symbols are as used in Table 1. The placement of + or ++ before or after the odor and light symbols indicates whether reinforcement was delivered before or after the presentation of these paired stimuli, respectively. If incentive contrast effects occur independently of a learned association between a reward and olfactory or visual stimuli, then the responses of subjects in the second session should depend only on the concentration of sucrose solution received in the first session. Subjects were not rewarded in the test.

Results

Figure 2 shows the acquisition curves for subjects in the two sessions. The performance of subjects in the first session depended only on whether proboscis extension was forward or backward conditioned. In particular, subjects trained on RG++ or RG+ responded to the delivery of the odor stimulus with proboscis extension more often than subjects trained on ++RG or +RG ($F(1, 76) = 207.78$, $p < 0.0001$). The performance of subjects in this session did not depend on the level of reinforcement ($F(1, 76) = 1.351$, $p = 0.2487$). In addition, the influence of the manner in which subjects were trained—proboscis extension forward or backward conditioned—did not depend on the magnitude of reward ($F(1, 76) = 0.47$, $p = 0.4876$).

The performance of subjects in the second session reveals an incentive contrast effect in the absence of any experience with cues that signal a reward. The repeated measures analysis of variance revealed that performance of all subjects increased over the second session ($F(1, 114) = 57.83$, $p < 0.0001$). But the performance of subjects trained on, or fed a high concentration of sucrose solution in the first session (RG++, ++RG, ++) performed less well than subjects initially trained on, or fed a low concentration (RG+, +RG, +) of sucrose solution ($F(1, 114) = 37.58$, $p < 0.0001$). There was no main effect of the history of exposure to olfactory and visual stimuli on performance ($F(2, 114) = 0.33$, $p = 0.7042$). No two-way or higher-order interactions were significant.

The reduced performance in the second session by subjects trained on, or fed a high concentration of sucrose solution in the first session cannot be attributed to satiety. In the test all 20 subjects trained on RG++ and 18 of the 20 subjects trained on RG+ responded to the odor and light conditions under which they were initially trained. These response frequencies do not differ significantly (Figure 2; Fisher's exact test, $p = 0.4871$).

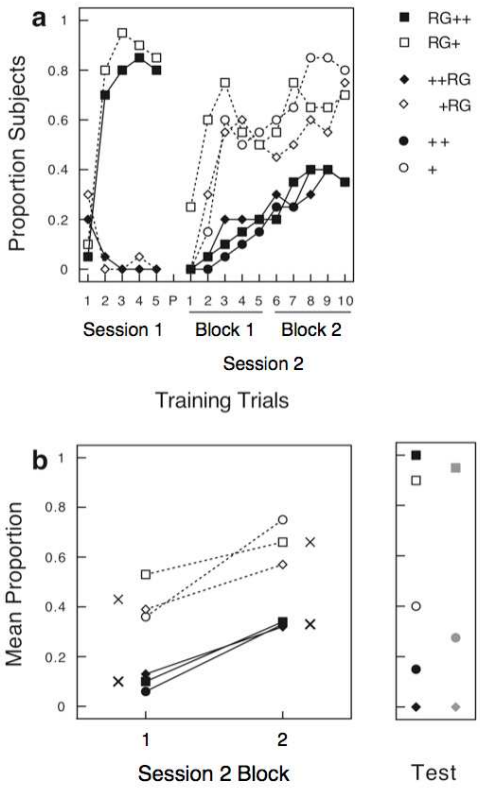

Figure 2. Acquisition curves and test responses of subjects in Experiment 2 reveal that the formation of reward expectations did not require a learned association between a reward and olfactory or contextual, visual stimuli. (**a)** Proportion of subjects that responded with proboscis extension to odor delivery in each trial of the first and second sessions. The intersession interval is indicated by P. (**b)** Mean response rate of subjects in the second session (divided into two equal blocks of five trials). Overall means for subjects that experienced a high (++) or low (+) concentration of sucrose solution in the first session are indicated by the symbols **x** and x, respectively. The gray symbols in the test results are the means of identically shaped open and solid symbols. Table 2 identifies legend symbols, which identify the treatment of subjects in the first session.

The test also reveals inhibition of responses by subjects trained in the initial session on ++RG or +RG. None of these 40 subjects responded in the test and this response frequency differs significantly from the response frequency of subjects trained in the first session on RG++ or RG+ (Fisher's exact test, $p < 0.0001$). Moreover, 11 of the 40 subjects fed + or ++ in the first session responded

in the test and this response rate is also higher than the response rate of subjects trained initially on ++RG or +RG (Fisher's exact test, $p = 0.0004$). The low rate of responses in the test by subjects trained initially on ++RG and +RG also reveals, as was observed in Experiment 1, the distinctiveness of the stimuli used in the two sessions.

Discussion

These experiments revealed that a reward reduction impedes performance, even if a substantive shift of the reinforcement context—the conditioned olfactory stimulus and static contextual cues—parallels the reduction of reward. Indeed, the results suggest that the formation of reward expectations does not require learned associations between olfactory and visual stimuli that predict a reward. Experience with a high concentration of sucrose solution, whether paired with olfactory and visual stimuli or provided unconditionally, in the absence of these stimuli, induced a similar performance decrement when subjects were later trained on a lower quality reward.

Two recent studies reveal that honey bees encode reward expectations in long term memory (Gil, De Marco, & Menzel, 2007; Gil, Menzel, & De Marco, 2008). But in incentive relativity experiments that involve a short temporal interval between the terminal experience with a high reward and the reduced reward experienced under test conditions, like those we conducted, any observed contrast effects could be ascribed, potentially, to *sensory adaptation* rather than to a process in which the secondary incentive is compared to a memory of the experienced incentive (Papini & Pellegrini, 2006). The low concentration sucrose reward used in the second session of each of our experiments may, for example, have been perceived as less sweet by subjects that experienced a reward reduction due to a sensory trace of the high concentration sucrose solution that carried over between sessions. Indeed, Biterman (1976) attributed his original observation of contrast effects in honey bees to this form of incentive relativity, which is now referred to as *sensory relativity* (Papini & Pellegrini, 2006).

More recent incentive contrast studies with honey bees reveal, however, decided evidence of a forceful disruptive process that is distinct from sensory relativity, even when high and low quality incentives are separated by time intervals of a few minutes (Couvillon & Bitterman, 1984). Honey bees trained on a high reward for an extended number of trials also show a reduced resistance to extinction relative to subjects trained over a shorter number of trials—the *overlearning extinction effect*—even when extinction trials are, likewise, conducted a few minutes after subjects are trained (Couvillon & Bitterman, 1980, 1984; Shinoda & Bitterman, 1987). These results discredit a purely sensory explanation of incentive contrast effects observed in experiments like those we conducted.

The results of our experiments with honey bees suggest that, as in vertebrates, neither conditioned nor static contextual stimuli have exclusive control over what is learned about the quality of a reward. Indeed, the control of reward expectations by contextual stimuli implicated in earlier studies with honey bees

and bumble bees and the behavior of subjects observed in this study are consistent with a simple mechanism, namely the comparison of a current incentive with an incentive experienced previously. Elucidation of the contributions of cued-recall relativity, recognition relativity and sensory adaptation to incentive contrast effects is an important objective for future studies of honey bee responses to shifts of a reward.

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Original received February 21, 2009.
Revision received July 24, 2009.
Accepted August 11, 2009.