

The Effects of Motivation on Extensively Trained Behavior

Yael Niv¹, Peter Dayan² and Daphna Joel³

¹ Interdisciplinary Center for Neural Computation
Hebrew University, Jerusalem 91904, Israel
yaelniv@alice.nc.huji.ac.il

² Gatsby Computational Neuroscience Unit, University College London
17 Queen Square, WC1N 3AR, London, UK
dayan@gatsby.ucl.ac.uk

³ Department of Psychology
Tel-Aviv University, Tel-Aviv 69978, Israel
djoel@post.tau.ac.il

Abstract

How motivation influences habitual behavior is unclear, since only motivational decrements have been considered. Here, in two experiments, we investigated the effects of motivational up-shifts and side-shifts on instrumental behavior which was extensively trained using a protocol known to promote habitual responding. In Experiment 1, hungry rats were trained to lever press for sucrose solution. Following a side-shift from food- to water-deprivation, rats showed less lever pressing in extinction compared to non-shifted controls, although a subsequent consumption test found no differences in sucrose consumption between thirsty and hungry groups. In Experiment 2, undeprived rats were trained to lever press for either sucrose solution or sucrose pellets. A post-training up-shift from satiety to water-deprivation did not affect lever pressing in extinction, regardless of outcome identity, although free consumption of sucrose solution, but not of pellets, was enhanced. Together, these results suggest that motivation affects extensively-trained instrumental behavior through a combination of general drive and generalization decrement, but not through determining the value

of the outcome. This is in stark contrast to the known effects of motivational states on moderately-trained (goal directed) behavior. The absence of an outcome-specific effect is in line with theories arguing for stimulus-response rather than response-outcome control of habitual behavior.

Introduction

A wealth of recent experiments has been devoted to the motivational control of conditioned behavior, revealing a rich and intricate tapestry of effects (for a recent review see Dickinson & Balleine, 2002). Contrary to the intuitive assumption that motivation modulates behavior directly, as has been suggested for Pavlovian responses (e.g., a hungry dog will salivate to a stimulus predictive of food, while a sated one will not, Mackintosh, 1974), a large body of evidence suggests that motivational states affect at least some classes of instrumental actions only indirectly. Specifically, motivational states affect moderately trained instrumental actions by determining the incentive value of the outcome of the behavior (Adams & Dickinson, 1981; Balleine, 1992; Lopez, Balleine, & Dickinson, 1992; Dickinson & Balleine, 1990, 1994; Dickinson, Balleine, Watt, Gonzalez, & Boakes, 1995; Balleine, Garner, Gonzalez, & Dickinson, 1995; Balleine & Dickinson, 1998, 2000; Dickinson & Balleine, 2002). This dependence on outcome value to mediate the effect of motivational states is explicit, in that the altered value needs to be experienced for the effects of a motivational shift to be manifest. For example, behavior aimed at acquiring food will be enhanced when hungry rather than sated, only if the subject has experienced the enhanced incentive value (desirability) of the food in this state (a process termed "incentive learning", cf. Dickinson & Dawson, 1988, 1989; Balleine, 1992, 2000). Such effects have been demonstrated for a wide range of motivational shifts – from hunger to thirst (Dickinson & Dawson, 1988, 1989), from thirst to hunger (Dickinson & Balleine, 1990; Balleine, 1992), from hunger to satiety (Balleine, 1992; Balleine et al., 1995; Balleine & Dickinson, 2000), from satiety to hunger (Balleine, 1992), from thirst to satiety (Lopez et al., 1992) and even using aversive motivational states (Henderson & Graham, 1979).

These results parallel those from a different line in experimentation, in which the value of the outcome is explicitly manipulated after training has commenced, albeit without changing the general motivational state of the animal. This is done, for instance, by conditioning taste aversion to the outcome through pairing its consumption with the induction of gastric illness (cf., Adams & Dickinson, 1981; Adams, 1982), or by inducing specific satiety through prefeeding of the outcome

(cf., Balleine & Dickinson, 1988, 2000; Killcross & Coutureau, 2003). When behavior is then tested in extinction, these studies show that given appropriate incentive learning, outcome devaluation causes a reduction in performance of moderately trained instrumental actions compared to non-devalued controls (Balleine & Dickinson, 1991, but see also Rescorla, 1992, 1994).

The fact that only *moderate* amounts of instrumental training are employed is especially noteworthy, because these latter studies also demonstrate that with *more extensive training* instrumental behavior can actually become *independent* of the value of its consequent outcome (Dickinson, 1985). Thus, when instrumental actions are over-trained, behavior becomes *insensitive* to post-training outcome devaluation, and subjects perform the trained action at comparable rates whether the outcome is devalued or not, regardless of incentive learning (i.e., even when they are given explicit experience with the outcome's modified value, cf. Adams, 1980; Dickinson, 1994; Killcross & Coutureau, 2003). This change in outcome sensitivity has been postulated to result from a shift in the underlying associative structure controlling behavior, from response-outcome (R-O) *goal-directed* (Tolman, 1949b), to stimulus-response (S-R, Thorndike, 1911) *habitual* control (Dickinson, 1985; Dickinson & Balleine, 1994; Dickinson et al., 1995; Balleine & Dickinson, 1998; Killcross & Coutureau, 2003, but see Colwill & Rescorla, 1985, 1986, 1988).

Taken together, these two lines of evidence raise a question regarding the nature of motivational control over extensively trained (habitual) behavior. As such behavior is in some important aspects autonomous of the value of its outcome, it is questionable whether motivational states will assert control through the modulation of outcome values, similar to the case of moderately trained behavior. To date, experimental investigations into this question have been largely confined to motivational *down-shifts*, that is, shifts from a motivated (e.g., hungry) to an unmotivated (e.g., sated) state. In one such study, Dickinson et al. (1995) trained hungry rats extensively to press a lever on a random interval schedule, in order to acquire food pellets. When tested in extinction, sated rats pressed the lever somewhat less than hungry rats, regardless of whether they had undergone incentive learning or not. To the contrary, response decrements in rats trained only moderately were dependent on incentive learning. Based on a small collection of such results, various authors have argued that motivational states control extensively trained actions directly, as in Pavlovian behavior, rather than through an alteration of the outcome value that necessitates explicit learning of the new value (Dickinson et al., 1995; Dayan & Balleine, 2002; Dickinson & Balleine, 2002; Killcross & Blundell, 2002). However, in the case of a motivational down-shift, results such as these can be interpreted differently.

Theoretically, there are several different routes by which shifts in motivation can modulate habitual behavior. Perhaps most intuitive is a **direct modulation** of the propensity to act, which could be dependent on the identity of the outcome, i.e., be **outcome specific**, as has been postulated in Pavlovian behavior (Dickinson & Balleine, 2002). Alternatively, as mentioned with respect to goal-directed behavior, motivational states can assert control over behavior through determination of the incentive value of the goals of behavior (“**incentive motivation**”, Tolman, 1949a, 1949b), such that behavior toward more valuable or desirable goals, would be enhanced, while that for less desired goals would be reduced. Important for our discussion, both these effects would manifest in the so called “directing” aspect of motivational control, which we will hitherto refer to as outcome-specific motivational control. Due to the apparent insensitivity of habitual behavior to outcome value this route of control may be unlikely, but it is nevertheless a theoretical possibility.

A second possible route to controlling behavior was proposed by Hull in his Generalized Drive hypothesis (e.g., Brown, 1961; Bolles, 1967) in terms of the “energizing” aspects of motivation. According to this, motivational states assert a certain “drive” which is applicable to many kinds of on-going behavior. Thus, as a result of **reduced general drive**, sated rats may be less inclined to perform *any* pre-potent action in the experimental situation, including lever-pressing. Importantly, this effect is not outcome-specific, but only dependent on the internal motivational state, such that general drive would be lower for satiety than for hunger, and a shift from satiety to hunger would be expected to have a non-specific enhancing effect on ongoing behavior, while a shift in the opposite direction would be expected to decrease ongoing behavior.

Last, post-training shifts in motivational state can influence behavior as a result of a **generalization decrement** from the learned context (which includes the motivational state which was in effect during training) to the context in effect when behavior is tested (Brown, 1961). Thus, and in accordance with an S-R controlled view of extensively trained behavior, the decrease in lever-pressing seen in Dickinson et al.’s (1995) study could have been mediated by the encoding of the motivational state in the S part of the S-R construct, and a **generalization decrement** from the training situation to the test situation. In essence, by changing the S, the S-R association will be activated to a lesser extent, resulting in attenuated responding (Dickinson & Balleine, 2002). Note that this effect is not only outcome-independent, but is also not dependent on the identity of the motivational state, as this last hypothesis predicts that *any shift in motivation*, even an up-shift from a non-motivated to a motivated state (such as from satiety to hunger), will induce a generalization decrement, which will result in a *reduction* in conditioned

	Down-Shift (hunger → satiety)	Up-Shift (satiety → thirst)	Side-Shift (hunger → thirst)
Outcome-Specific (directing effect)	↓	↔ or ↑ pellets solution	↓ or ↔ pellets solution
General Drive (energizing effect)	↓	↑	??
Generalization Decrement	↓	↓	↓

Table 1: Possible effects of motivation on behavior, and their prediction for extensively trained instrumental behavior tested after motivational down-shifts, side-shifts and up-shifts. Arrows illustrate a reduction, increase, or no predicted change in rate of behavior as compared to unshifted controls. Note that the prediction regarding the drive effect for the side-shift is underdetermined, as there is no clear independent measure of the relative drive induced by hunger versus thirst. For simplicity, and as both effects are presumably outcome-specific and thus have similar predictions for behavior, direct control and control through determining the incentive motivation of the outcome have been combined.

behavior (Brown, 1961).

These potential effects of a motivational shift are not at all mutually exclusive. However, they may predict different directions of change of behavior, as a result of their different dependencies on the identity of the outcomes and motivational states. Table 1 illustrates the predictions of these effects for qualitatively different motivational shifts - a down-shift from a deprived to an undeprived state (e.g., from hunger to satiety), an upshift from an undeprived to a deprived state (e.g., from satiety to thirst), and a side-shift between two different deprivation states (e.g., from hunger to thirst). Predictions are illustrated for behavior trained with either sucrose pellets (relevant to food-deprivation only) or sucrose solution (relevant both to a food deprived and a water deprived state).

Clearly, a motivational down-shift confounds the above three hypotheses, as they all predict a reduction in behavior. Thus, to obtain a satisfactory answer as to the nature control of extensively trained behavior by motivational states, in the present study we tested the effects of motivational side-shifts and up-shifts on extensively trained lever pressing. Our aim was to contrast and differentiate between the three qualitatively different hypotheses laid out above, in order to clarify the nature of motivational control over habitual behavior. Because we were particularly interested in the effects of motivation on that instrumental behavior which is independent of the value of the outcome, we used a training protocol specifically aimed at promoting habitual behavior – in accordance with Adams (1982),

Dickinson and Nicholas (1983b), and Holland (2004), we trained rats to perform a single action in order to obtain a single outcome, using a random-interval schedule of reinforcement, and training for fifteen sessions. Furthermore, we sought to minimize any influence of Pavlovian motivational effects on our results, for instance via control exerted by the context (e.g., a motivational shift can affect factors such as the Pavlovian approach to the lever which would then indirectly affect instrumental lever-pressing, Dickinson & Nicholas, 1983a; Dickinson & Dawson, 1987). A standard route to eliminating the effect of these is to compare responding on two different levers trained in the same context for two different outcomes (one the motivational target). This equates Pavlovian contextual influences, thus allowing the instrumental outcome-dependent performance to be isolated (cf. Dickinson & Dawson, 1989). Unfortunately however, training two actions for two outcomes has been shown to produce behaviour resistant to habituation (Holland, 2004). Therefore, following Coutureau and Killcross (2003), we used post-training “context extinction” sessions. In these, the animals were put in the training chamber in the absence of levers and of outcomes, thus extinguishing Pavlovian associations between the experimental context and the outcome while avoiding extinction of the instrumental behaviour.

Experiment 1: Motivational side-shift

Food-deprived rats were extensively trained to lever-press for a sucrose solution outcome. They were then tested under extinction conditions while either food-deprived (group HUNGRY) or water-deprived (group THIRSTY). Importantly, the sucrose solution was a motivationally relevant outcome in both these deprived states, as a result of its liquid as well as nutritional properties. This design allowed us to differentiate between an outcome-dependent form of motivational control, according to which there should be no change in the behavior, since as the outcomes were relevant to both the training and the test motivational states, and the generalization decrement hypothesis which predicts a decrease in conditioned behavior as a result of the motivational shift itself. The effect of general drive could not be determined in this experiment, as although all rats were tested in a deprived state, the precise amount of drive induced by water deprivation as compared to that induced by food deprivation is unknown. Note that we used a shift from hunger to thirst, rather than from thirst to hunger, as previous studies have shown that water deprived rats reduce consumption of the dry lab chow, and thus, over time, are also food-deprived (Dickinson & Balleine, 1990). By depriving the rats of water for only one day prior to the test, it is likely that the dominant deprivation was that of water rather than food. See table 2 for a summary of the

	Training (15 sessions)	Test (extinction)
Exp. 1	Hungry: LP (RI30) → sucrose solution	Hungry or Thirsty
Exp. 2	Sated: LP (RI30) → sucrose pellets or solution	Sated or Thirsty

Table 2: Design of Experiments 1 and 2. LP=lever press; RI=random interval schedule. RI30 refers to the RI schedule in effect during the extended phase of training

design of this experiment.

Materials and Methods

Subjects

Fourteen male Sprague Dawley rats (Harlan Laboratories, Jerusalem, Israel) approximately three months old, weighing 329-473 grams (mean 362g) were housed 3-4 to a cage, in a vivarium maintained on a 12-hour light-dark cycle (lights on 15:00-3:00). All behavioural training and testing occurred during the dark portion of the cycle. Animals were allowed one month familiarisation with the vivarium before training began. During training, rats were maintained on a 22-hour food restriction schedule, with tap water available *ad lib* in the home cage. Under this schedule, food (standard lab chow) was provided in the home cage for two hours each day, always after the daily treatment/session. The rats were weighed twice a week to ensure that their body weight was not reduced to below 90%. During testing half of the rats were shifted to a 23-hour water restriction schedule (see below), with food freely available, while the rest were maintained on the food restriction schedule. All animal research was carried out according to the guidelines of the Institutional Animal Care and Use Committee of Tel Aviv University. All efforts were made to minimise the number of animals used and their suffering.

Apparatus

Behavioural training and testing was conducted in four operant chambers (Camden Instruments, Loughborough, UK) fitted with a recessed food magazine and two retractable levers. The levers were 4 cm wide and were positioned 2.8 cm from the side walls, 7.5 cm from either side of the food magazine, and 5 cm from

the grid floor. Only the left lever was used in this experiment, and the right lever remained retracted at all times. The chambers could be illuminated by a house-light located at the ceiling. Access to the food magazine was through a hinged Perspex panel, the opening of which activated a microswitch. A peristaltic pump (RS Components, Northants, UK) attached to a silicon tube inaccessible to the rats, delivered approximately 0.25ml of 20% sucrose solution (hand mixed) into the food magazine, over a period of 1 second. The operant chambers were housed in sound-attenuating boxes, and ventilating fans were mounted on the side of each box. Equipment programming and data recording were computer controlled by ABET software (Lafayette Instrument Co., Indiana, USA). The consumption test took place in individual feeding cages made of white plastic measuring 13x13x30cm, with wire-mesh ceilings, which were fitted with plastic bottles containing sucrose solution. The bottles and their location in the wire mesh were similar to those used for providing water in the home cage.

Procedure

Handling On Days 1-3, rats were individually handled for about 2 minutes daily. A 22-hour food restriction schedule began one day prior to handling, and continued throughout subsequent training (until Day 20). In order to reduce neophobia to the sucrose solution, after each daily handling session and prior to the daily feeding, rats were pre-exposed to sucrose solution in their home cages for ten minutes. A small plastic dish containing 20% sucrose solution was placed in the home cage. All rats were observed to consume solution in the ten-minute exposure.

Rats were then divided into two groups – group HUNGRY would be tested when food deprived as in training, while group THIRSTY would be tested after a shift from food deprivation to water deprivation.

Magazine training. On Days 4-5, rats were trained to consume sucrose solution from the food magazine in the operant chamber, with the lever retracted. The session began with the onset of the house-light, which remained on for the entire session. Sucrose solution was delivered into the food magazine on a random time schedule, with a uniformly variable delay of 30-90 seconds (mean 60 seconds). On Day 4, the magazine flap was taped back so that the magazine was constantly open and the sucrose solution was easily reachable. Training continued until twenty-five outcomes were delivered, after which the session ended and the house-light was turned off. On Day 5, the session ended after twenty outcomes had been collected (as measured by the insertion of the rats' head into the food

magazine), or until twenty-five outcomes had been delivered. The number and timing of head insertions into the food magazine were recorded.

Lever-press training. On Days 6-18, rats were trained to lever-press in order to obtain sucrose solution in a free operant procedure. The beginning of each session was signalled by the onset of the house-light and the insertion of the left lever. On Day 6, every press on the lever delivered an outcome into the food magazine. Individual shaping was used in this session to assist in acquisition of the lever-press response. On Days 7-18, a random interval schedule of reinforcement was introduced, in which an outcome was delivered only for the first lever-press after the programmed interval had elapsed. The mean interval was 2 seconds on Day 7, 15 seconds on Day 8, and 30 seconds for the following twelve training sessions. Reinforcement was equally likely in the interval starting from half the nominal value of the schedule and ending after 150% of the nominal value of the schedule had elapsed. Immediately after the delivery of an outcome, a new interval within these boundaries was drawn, and the interval timer was started. All sessions terminated when thirty outcomes had been delivered, except the session on day 6 which ended when thirty outcomes had been collected (as measured by insertion of the rat's head into the food magazine prior to the delivery of the next outcome), or when forty outcomes had been delivered. The lever was then withdrawn, and the house-light was turned off. Days 12 and 15 included two training sessions each, separated by at least one hour, such that overall, a total of fifteen lever-press training sessions were given over thirteen days. Both lever presses and head insertions into the food magazine were recorded.

One rat in group HUNGRY refused to consume the sucrose solution from the food magazine, and was dropped from the study. Another two rats required extra days for magazine training and/or lever press training, and thus received only seven sessions of training on the 30sec random interval schedule, instead of twelve. Results omitting these rats were no different from those reported below, and thus they were not omitted from the study. This resulted in final Ns of 6 rats in the HUNGRY group and 7 rats in the THIRSTY group.

Context extinction. On Days 19-20, all rats underwent three sessions of context extinction. The sessions began with the onset of the house-light and were terminated twenty minutes later with its offset. Throughout these sessions, the levers were retracted and no outcomes were given. Two sessions were given on Day 19, separated by at least one hour, and one session was given on Day 20. Note that these sessions did not extinguish the learned lever-press behavior, as the lever was not available for pressing.

Motivational shift. Immediately after the last context extinction session (i.e., on

Day 20), food and water were returned to the home cages for 24 hours. The next day (Day 21), water was removed from the home cages of group THIRSTY, and food was removed from the home cages of group HUNGRY. This procedure was intended to ensure that the rats on a water-deprivation schedule in test did not also remain food-deprived as a result of low consumption of the dry lab chow in the absence of water. Thus all rats were allowed to consume food and water *ad lib* for one day before the appropriate test deprivation state was established.

Extinction and Consumption tests. On Day 22, after at least twenty-two hours of food/water deprivation, rats were tested for lever-pressing behavior in extinction. The test session started with the onset of the house-light and the insertion of the left lever, and resumed fifteen minutes later with the retraction of the lever and the offset of the house-light. Lever pressing had no programmed consequences in this session, and no outcomes were delivered throughout. Lever pressing and head insertions into the food magazine were recorded. Immediately after the extinction test, a consumption test ensued. Rats were placed in individual cages and allowed to drink sucrose solution freely from a plastic bottle, for an hour. The amount of sucrose consumed was computed by weighing the bottles before and after the test.

Statistical Analysis

Unless otherwise stated, analysis of the results was performed using one-way analysis of variance (ANOVA), with a main factor of group. An alpha level of 0.05 was used to assess the statistical significance of the results.

Results and Discussion

In the last session of lever-press training, both groups exhibited similar response rates (mean (SD) lever-press rates for groups THIRSTY and HUNGRY were 20.4(5.6) and 17.7(5.5) presses per minute, respectively; mean (SD) rates of magazine entry were 13.7(3.9) and 16.4(10.0) entries per minute, respectively, all $F_s < 1$).

The consumption test showed that the amount of sucrose consumed was similar in both groups (Figure 1a; $F(1, 11) = 1.45$, $P > 0.25$), suggesting that the sucrose solution could be regarded as a motivationally relevant outcome for both the food-deprived and the water-deprived groups.

The results of prime interest are from the extinction test. Figures 1b and 1c show the lever-press and magazine entry results from this test stage. In order to re-

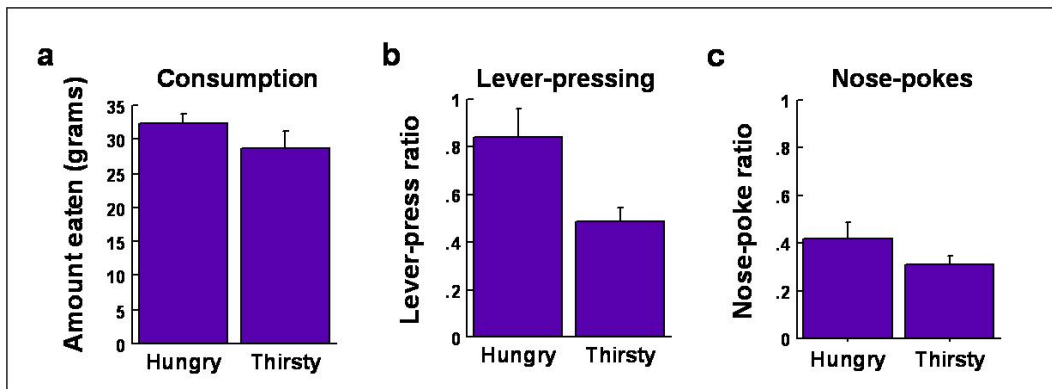


Figure 1: (a) Mean amount (in grams) of sucrose solution consumed by each of the two groups in the consumption test. (b) Mean rate of lever pressing in each group in the extinction test, expressed as a percentage of lever press rate in the last training session. (c) Mean rate of magazine entries in each group in the extinction test, expressed as a percentage of magazine entries in the last training session.

duce between-subject variability, response rates were expressed as a percentage of the responding in the last training session. As can be seen, there were no differences between the groups in the rate of magazine entry during the test (Figure 1c; $F(1, 11) = 2.1, P > 0.15$). In contrast, water-deprived rats showed *less* lever-press responding than food-deprived rats (Figure 1b; $F(1, 11) = 8.3, P < 0.05$).

Although the consumption results showed no significant differences between treatment groups, there was a small tendency of the shifted rats to consume less sucrose solution than the non-shifted controls. In order to assess whether the effect of the motivational shift on lever-pressing behavior was confounded by this tendency, an analysis of covariance (ANCOVA) was performed on the lever-press data using the amount eaten as covariate. This analysis yielded a similar main effect of group ($F(1, 10) = 6.99, P < 0.05$).

These results show that rats that had undergone a motivational shift between training and testing *reduced* their instrumental lever-press performance compared to rats whose motivational state had not been shifted, although they did not reduce their subsequent consumption of the sucrose solution. The finding that the difference between the groups was significant also when using the amount of sucrose consumed as a covariate, indicates that differences in the “desirability” of the outcome cannot account for the reduced rate of lever-pressing in the water-deprived group. Moreover, this reduction cannot be explained by a competition between lever-presses and magazine responses, because, if anything, the shifted group tended to perform slightly less magazine behavior than the control group.

The reduction in lever-pressing is in line with the generalization decrement hypothesis, rather than an outcome-value dependent modulation of behavior by motivation. As stated before, in the absence of an independent measure of the drive asserted by the food deprived and the water deprived states, we cannot make any affirmative conclusions regarding the role of drive in this experiment.

Experiment 2: Motivational up-shift

Experiment 1 provided support for the generalization decrement hypothesis, however, as mentioned, it could not provide evidence for or against the general drive hypothesis, and it could not provide conclusive evidence against the outcome specific hypothesis as only one outcome was used. In order to further investigate the role of these in the motivational control of extensively trained behavior, Experiment 2 studied the effects of a motivational up-shift on behavior trained with one of two different outcomes. Rats which were neither food deprived nor water deprived were trained to lever-press for either sucrose pellets or sucrose solution, and tested under extinction conditions with half the rats shifted to a water-deprived state (groups PEL/THIRSTY and SOL/THIRSTY) and half the rats tested in a nondeprived state (groups PEL/SATED and SOL/SATED). Importantly, as a result of its liquid property, the shift to water deprivation was intended to enhance the value of the sucrose solution for group SOL/THIRSTY compared to that for non-deprived rats (group SOL/SATED), while not affecting the value of sucrose pellets, which should be similarly desirable for shifted and non-shifted rats (groups PEL/THIRSTY and PEL/SATED respectively). Outcome-specific motivational control of behavior would thus predict an increase in behavior in the shifted rats trained with solution, but no change in the behavior of the rats trained for pellets. Note that only a different pattern of results for the two outcomes could attest to truly outcome-specific control.

The motivational upshift also provides a testable prediction regarding the effect of general drive. In this scenario, water deprivation should clearly induce more general drive than a nondeprived state, thus if general drive plays a significant role in the motivational control of extensively trained behavior, water-deprived rats should elevate their responding compared to non-deprived rats. This effect should be outcome independent. In contrast, the generalization decrement hypothesis predicts the opposite direction of change – a reduction in behavior as a result of the motivational upshift, again, regardless of the identity of the outcome for which the animals are working, or its relevance to the deprived motivational state. See Table 2 for a summary of the design of this experiment.

Materials and Methods

Subjects

Twenty male Sprague Dawley rats (Harlan Laboratories, Jerusalem, Israel) approximately three months old, weighing 323-389 grams (mean 361 g) were housed four to a cage, in the same vivarium described in experiment 1. Animals were allowed one month familiarisation with the vivarium before behavioural training began. Throughout training, rats were maintained with tap water and standard lab chow available *ad lib*. During testing half of the rats were shifted to a 23-hour water restriction schedule (see below), with food freely available. All animal research was carried out according to the guidelines of the Institutional Animal Care and Use Committee of Tel Aviv University. All efforts were made to minimise the number of animals used and their suffering.

Apparatus

The apparatus was the same one used in Experiment 1. In addition to the use of the peristaltic pump to deliver sucrose solution, a pellet dispenser delivered 45-mg, "dust-free" sucrose pellets (Noyes, Sandown Chemical Limited, Hampton, England) into the same food magazine. Familiarisation with sucrose pellets took place in the home cages, where pellets were placed in a small plastic dish. The consumption test took place in the individual feeding cages described in experiment 1, which were either fitted with plastic bottles containing sucrose solution or contained small plastic dishes in which sucrose pellets were placed.

Procedure

Handling. On Days 1-3, rats were individually handled for about 2 minutes daily. In order to reduce neophobia to sucrose, after each handling session a small plastic dish containing approximately 30 sucrose pellets was placed in the home cage. The dish was removed from the cage after each rat was observed to consume at least two pellets.

Rats were then divided into two groups – group PEL would be trained with one sucrose pellet as an instrumental outcome, while group SOL would be trained with approximately 0.27ml 20% sucrose solution as an outcome. The pure sucrose content of the pellet and the solution outcomes were approximately the same.

Magazine training. On Days 4-5, rats were trained to consume their respective outcomes from the food magazine in the operant chamber, as described for experiment 1.

Lever-press training. On Days 6-18, rats were trained to lever-press in order to obtain their respective outcome, in a free operant procedure, as described for experiment 1.

One rat in the SOL group did not acquire magazine entry behavior and was dropped from the study. Another two rats in the SOL group required extra days for magazine training and/or lever press training, and thus received only six and nine sessions of training on the 30sec interval schedule respectively, instead of twelve. Results omitting these rats were no different from those reported below, and thus they were not omitted from the study.

Context extinction. On Days 19-21, rats underwent three sessions of context extinction (one session a day), as described for experiment 1.

Motivational shift. Immediately after the last context extinction session (i.e., on Day 21), water was removed from the home-cages of half of the rats in each of the two groups. This resulted in four groups: groups SOL/THIRSTY (N=5) and PEL/THIRSTY (N=5) – to be tested when water deprived, and groups SOL/SATED (N=4) and PEL/SATED (N=5) – to be tested undeprived.

Extinction and Consumption tests. On Day 22, after at least twenty-two hours of water deprivation, rats were tested for lever-pressing behavior in extinction as described for experiment 1. Immediately after the extinction test, a consumption test ensued. Rats in groups SOL/THIRSTY and SOL/SATED were placed in individual cages and allowed to drink sucrose solution freely from a plastic bottle, for an hour. The amount of sucrose consumed was computed by weighing the bottles before and after the test. Rats in groups PEL/THIRSTY and PEL/SATED were placed in individual cages and allowed to consume sucrose pellets freely from a small plastic dish in the cage, for an hour. The amount consumed was computed by weighing the cage (without the rat) before and after the test.

Statistical Analysis

Unless otherwise stated, analysis of the results was performed using two-way analysis of variance (ANOVA), with main factors of motivation and outcome identity. An alpha level of 0.05 was used to assess the statistical significance of the results.

Results and Discussion

In the last session of instrumental training, both PEL groups showed similar response rates (mean (SD) rates of lever pressing in groups PEL/SATED and PEL/THIRSTY were 7.6(3.8) and 7.6(3.2) presses per minute, respectively; mean (SD) rates of magazine entry were 6.7(4.3) and 8.1(4.1) entries per minute, respectively), and both SOL groups showed similar response rates (mean (SD) rates of lever pressing in groups SOL/SATED and SOL/THIRSTY were 6.8(3.2) and 6.8(3.0) presses per minute, respectively; mean (SD) rates of magazine entry were 4.8(1.6) and 5.7(2.9) entries per minute, respectively). Statistical analysis showed no significant main effects or interactions (all $F_s < 1.7$, $P_s > 0.2$). However, as the groups trained with sucrose solution as an outcome showed a tendency to respond less than those trained with sucrose pellets, and in order to reduce between-subject variability, response rates in the extinction test were expressed as a percentage of response rates in the last training session.

The results from the consumption test confirmed that the motivational upshift had indeed produced the desired effect on the values of the different outcomes. Figure 2a shows the amount of outcome (sucrose pellets or sucrose solution) consumed in the consumption test, by all four groups. Clearly more sucrose solution was consumed (as measured by weight) than were sucrose pellets. However, the result of interest is that the PEL/THIRSTY groups consumed the same amount of pellets as the PEL/SATED group, whereas the SOL/THIRSTY group consumed *more* solution than the SOL/SATED group. This is in accord with the prediction that the sucrose solution would be more desirable for water-deprived rats as compared to non-deprived rats, while sucrose pellets, lacking the liquid property, would not be. These observations were confirmed by statistical analysis, which showed significant main effects of outcome ($F(1, 15) = 151.4$, $P < 0.0001$) and motivation ($F(1, 15) = 7.4$, $P < 0.5$), and a significant outcome x motivation interaction ($F(1, 15) = 14.1$, $P < 0.005$).

In spite of the higher motivational relevance of the sucrose solution to the water-deprived rats, the lever-press results from the extinction test (Figure 2b) show that the SOL/THIRSTY group *did not* press the lever any more than the other groups. If anything, the water-deprived rats trained with sucrose solution tended to press the lever *less* than the non-deprived rats. This result, however, did not reach statistical significance (all $F_s < 1$ in a two-way ANOVA).

As can be seen in Figure 2c, results for the magazine entry behavior were more reflective of the value of the different outcomes to the different groups, as there was a tendency of the SOL/THIRSTY rats to perform more food magazine entries than the

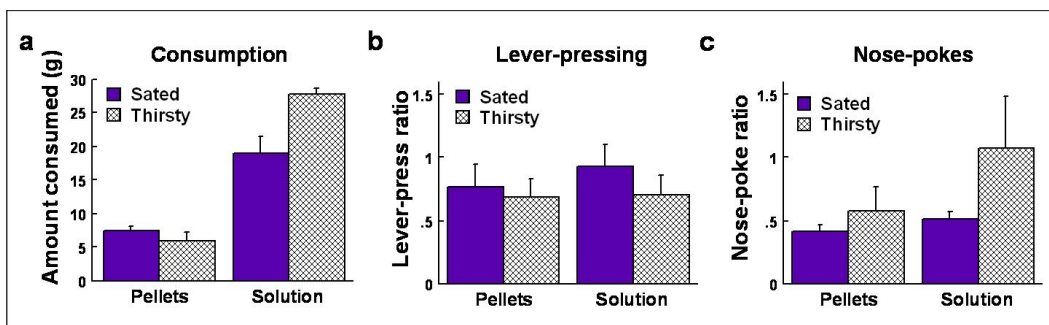


Figure 2: (a) Mean weight (in grams) consumed by each of the four groups in the consumption test. (b) Mean rate of lever pressing in each group in the extinction test, expressed as a percentage of lever press rate in the last training session. (c) Mean rate of magazine entries in each group in the extinction test, expressed as a percentage of magazine entries in the last training session.

other groups. However, the results failed to reach significance (all $P_s > 0.15$ in a two-way ANOVA). Nonparametric tests used as a result of the difference of variances between shifted and non-shifted groups yielded similarly non-significant results. That the outcome-specific effect on magazine entry behavior did not reach significance may be the result of the context extinction procedure – Coutureau and Killcross (2003), who applied six sessions of context extinction, also failed to show the previously well-documented effect of outcome devaluation by specific-satiety prefeeding on magazine behavior (even after extensive training, cf., Killcross & Coutureau, 2003), a negative finding that they attributed to the addition of the context extinction stage.

General Discussion

Balleine (1992) investigated the effects of motivational up-shifts and down-shifts on moderately trained goal-directed lever-pressing for food, and found that post-training motivational shifts modulate goal-directed behavior by means of determining the value of the goal of the behavior. Here we conducted a similar investigation into the control of extensively trained lever-pressing by motivational states, in order to elucidate the motivational control of habitual behavior.

In experiment 1 we trained rats extensively to lever-press for a sucrose solution while hungry, and then subjected half the rats to a motivational side-shift from food deprivation to water deprivation, and compared lever-pressing in extinction

to that of non-shifted rats. Although a consumption test showed that the outcome was as desirable in the thirsty as in the hungry state, rats shifted to thirst before testing pressed the lever significantly less than unshifted controls. The rate of magazine behavior, however, was not significantly lower in the shifted group compared to the unshifted group.

Experiment 2 employed an upshift from a non-deprived to a water-deprived state, and compared lever pressing in extinction of rats trained extensively with either sucrose pellets or sucrose solution as an outcome. A consumption test showed the solution outcome to be more valued in the deprived compared to the non-deprived state, while the pellets were similarly desirable in both states. Regardless of the different outcome values, lever pressing in both shifted groups was not significantly different from that of unshifted controls. In contrast, the rate of magazine behavior did show a tendency to follow the new outcome values, although this result did not achieve statistical significance.

Taken together, these results suggest several conclusions regarding the effects of motivation on extensively trained behavior. First and foremost, no outcome-specific motivational effects on lever-pressing were found in either experiment. Thus our results show that the motivational control over extensively trained lever-pressing is *not* mediated by alterations of the value of the outcome. This is not surprising given that we chose to investigate that specific behavior which is known to be independent of the value of its consequent outcome (Dickinson, 1985). Furthermore, the results of both experiments are consistent with a combined effect of general drive and generalization decrement on habitual lever-pressing. In experiment 1 drive is probably more or less equated, and an effect of generalization decrement as a result of the motivational shift can be clearly observed. The absence of this generalization decrement effect on lever-pressing in the shifted groups in experiment 2 is explained by assuming the *summation* of two opposing effects – a general drive effect elevating responding in the water deprived groups, and a generalization decrement effect reducing responding in these same groups as a result of the motivational shift.

The pattern of effects of motivational shifts on lever-pressing obtained in the present experiment is qualitatively different from that well documented for moderately trained, goal-directed behavior, which instead displays outcome-dependent indirect effects of motivation. It could be argued that the lack of outcome-dependent effects of motivation in the present experiments results from the absence of an incentive learning stage, as this has been shown to be crucial for the effects of motivation on moderately trained behavior. However, two lines of evidence lead us to believe that this is not the case. First, previous outcome devaluation

studies have shown that incentive learning does not affect extensively trained behavior (Adams, 1980, 1982; Dickinson et al., 1995) and have demonstrated the outcome-independent nature of this behavior, already suggesting the lack of outcome-dependent effects of motivation. Furthermore, in the absence of incentive learning, moderately trained behavior does not show either the generalization decrement or the general drive effects seen here (Balleine, 1992; Balleine et al., 1995; Dickinson et al., 1995; Lopez et al., 1992). We therefore suggest that the different effects of motivation on moderately versus extensively trained behavior are, in fact, indicative of the different nature of these two types of behavior, and their different underlying control structures, as will be discussed below.

Interestingly, the results for lever-pressing in the present experiments were also different from those of the magazine head-insertion responses. In contrast to the outcome independence of lever-pressing, in both experiments the rate of magazine behavior tended to follow the value of the outcome in the different motivational states, as assessed in the consumption tests. This accords with several recent studies which show direct, outcome-specific effects of devaluation or motivational shifts on magazine behavior, regardless of amount of training (cf. Balleine & Dickinson, 1991; Balleine, 1992; Killcross & Coutureau, 2003).

Such diversity of motivational effects is in line with the division of conditioned responses into three distinct classes, namely, Pavlovian responding, goal-directed actions, and habitual behavior. In the following, we first discuss the implication of the observed effects of motivation on extensively trained lever-pressing, for the associative control over habitual behavior, and particularly, for the debate as to whether extensively trained behavior indeed shifts from goal-directed R-O control to habitual S-R control. We then consider possible explanations for the apparent resistance to habitization of magazine behavior.

In the debate regarding the associative control of extensively trained instrumental behavior, one claim, made by Dickinson and colleagues, is that overtraining breeds habits which are *not* performed in order to obtain their consequent outcomes. Rather, in a form of S-R control, these are elicited by the stimuli in the presence of which they were trained, and are fairly autonomous of the value of their outcomes (Dickinson, 1985; Dickinson et al., 1995; Dickinson, Squire, Varga, & Smith, 1998; Dickinson & Balleine, 2002; Dayan & Balleine, 2002; Killcross & Coutureau, 2003). This view builds on findings showing insensitivity (or reduced sensitivity) of extensively trained behavior to post-conditioning devaluation of outcomes (Adams & Dickinson, 1981; Adams, 1982; Yin, Knowlton, & Balleine, 2004), and reduced sensitivity to post-training changes in action-outcome contingencies (Dickinson et al., 1998).

The alternative claim, espoused by Rescorla and colleagues, is that overtraining not only does not reduce R-O control, but to the contrary – the role of the R-O association becomes more pronounced as training proceeds (for a review see Colwill & Rescorla, 1986). This view builds on studies that show that irrespective of extended training, instrumental responding remains under the control of the outcome as assessed by post-training devaluation of the outcome (Colwill & Rescorla, 1986, 1988), and outcome-specific Pavlovian-instrumental transfer (Colwill & Triola, 2002). However, these latter studies have all employed training procedures which involve performing at least two different actions in order to obtain two or more different outcomes (Colwill & Rescorla, 1986), a feature that may serve to enhance the encoding and usage of outcome-specific attributes (Dickinson, 1985; Dickinson et al., 1995). A recent Pavlovian-instrumental transfer study which specifically tested this assumption, has provided direct support for such a multiple-outcomes-induced difference in the structures controlling instrumental behavior (Holland, 2004). Thus, it seems that training using multiple actions and outcomes results in behavior which is actually resistant to habitization and to the transfer of control to an S-R structure.

Our study supports the hypothesised S-R control of habitual behavior. We used a training protocol specifically aimed at producing habitual behavior, and indeed showed that, contrary to the outcome-mediated motivational control of goal-directed behavior, the motivational control of habitual behavior is outcome independent. Furthermore, the prominent role for generalization decrement is in accord with an S-R view of habitual control, as this view stresses the importance of the stimulus S in the presence of which the behavior was learned, in eliciting conditioned habitual behavior. Changes in S (which, in a free operant task, is usually identified with the contextual stimuli) will have a profound effect on the response R, if this is indeed the controlling structure. It would not be surprising to find a lesser role for generalization decrement in goal-directed behavior, as there the stress is on associations between the response and the outcome as controlling behavior, rather than the contextual stimuli. It is interesting that in both cases a prominent route to motivational control over behavior is through the constituents of the association controlling behavior: in R-O controlled goal-directed behavior, motivation asserts control through the O, while in S-R controlled habitual behavior, control is asserted through the S, suggesting that motivation may not have a privileged route through which it affects behavior.

The effect of general drive on habitual behavior is easily incorporated into such a theory of behavioural control. Assuming that the vigour of goal-directed behavior is determined, among other factors, by the value of the outcome, and given that habitual behavior is autonomous of this value, the question arises as to what con-

trols the vigour of habitual behavior? As postulated by Hull (1943), our results are indicative of an outcome-independent control of rate of habitual responding by the general drive induced by the animal's motivational state.

On the other hand, the apparent outcome-specific incentive motivation effects on magazine behavior, even in face of extensive training which normally renders instrumental behavior insensitive to outcome value, have been taken to suggest that magazine behavior is not predominantly an instrumentally controlled behavior, but rather a Pavlovian approach-type response (Balleine & Dickinson, 1991; Balleine, 1992, 2000; Dickinson & Balleine, 2002; Dayan & Balleine, 2002). This has also been one of the major lines of evidence for the direct motivational control of Pavlovian responses. Two studies contest this interpretation. Balleine and colleagues (Balleine et al., 1995; Corbit & Balleine, 2003) examined motivational control in rats performing a chain of two purely instrumental responses (e.g., lever pressing followed by chain pulling) in order to obtain reward, without the need for a consecutive magazine-flap response in order to gain access to the food itself. They found that after moderate training (or training on a ratio schedule of reinforcement known to produce behavior relatively resistant to habitization), the response more proximal to the reward was directly affected by a motivational shift, whereas the effect of the motivational shift on the distal response necessitated incentive learning. Moreover, when trained to lever-press without the need for a magazine-flap response in order to obtain the food, lever-pressing itself showed such immediate motivational effects (although incentive learning further augmented these (Balleine et al., 1995), and see also Rescorla, 1994).

These results suggest that a major factor in determining susceptibility to direct outcome-dependent motivational influence, even in light of extensive training and in the absence of an opportunity for incentive learning, may be the *proximity* of the response in question to the outcome, rather than its Pavlovian or instrumental nature (Dickinson, Nicholas, & Adams, 1983; Rescorla, 1994; Killcross & Blundell, 2002). According to this view, instrumental actions proximal to the outcome may be directly sensitive to the value of the outcome, while distal actions necessitate incentive learning in order to show the effects of motivation early in training, and are rendered insensitive to outcome value with extensive training (Daw, Niv, & Dayan, In Press). Thus the magazine entries in our study may have shown outcome-dependent effects of motivational shifts by virtue of their proximity to the outcome itself. Moreover, our results extend the observation of direct motivational control of proximal actions to the case of motivational up-shifts and side-shifts, as previous studies exclusively examined down-shifts in outcome value. Interestingly, there may be evidence for an analogous proximal-distal distinction in the effects of outcome devaluation on purely Pavlovian responses (Holland &

Straub, 1979). Measuring several different conditioned responses to a cue predicting food, these authors showed that post-conditioning outcome devaluation resulted in a significant reduction of responses more proximal to the outcome, while distal responses were not affected. This again raises the question as to the precise nature of motivational control over Pavlovian responses.

To summarise, conditioned behavior can be crudely divided into Pavlovian responses, goal-directed instrumental actions, and habitual behavior. This tripartite division is also manifest in the different effects of motivation on the three classes of behavior (Dickinson & Balleine, 2002; Dayan & Balleine, 2002). Although it is known that motivation exerts control over moderately trained goal-directed behavior by determining the incentive value of its consequent outcomes, the motivational control of extensively trained behavior was previously not well determined. Here we have shown that motivation does not impose any form of outcome-specific control on extensively trained (and likely habitual) behavior. However, our results show that motivational states can control the vigour of habitual behavior through their general drive properties, and, furthermore, that shifts in motivational states influence habitual behavior as a result of generalization decrement.

Acknowledgements

We are grateful to Anthony Dickinson, Bernard Balleine, Nathaniel Daw, Sanne De Wit and Peter Holland for beneficial discussions, and particularly to Bernard Balleine and Sanne De Wit for helpful advice regarding the experimental design and setup and for comments on an earlier draft. This work was funded by a grant from the Interdisciplinary Center for Neural Computation, Hebrew University, Jerusalem, and by the Gatsby Charitable Foundation.

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