Resolution of Conflict Between Goal-Directed Actions: Outcome Encoding and Neural Control Processes

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According to O-R theory of instrumental learning, incongruent biconditional discriminations should be impossible to solve in a goal-directed manner because the event acting as the outcome of one response also acts as a discriminative stimulus for an opposite response. Each event should therefore be associated with two competing responses. However, Dickinson and de Wit (2003) have presented evidence that rats can learn incongruent discriminations. The present study investigated whether rats were able to engage additional processes to solve incongruent discriminations in a goal-directed manner. Experiment 1 provides evidence that rats resolve the response conflict that arises in the incongruent discrimination by differentially encoding events in their roles as discriminative stimulus and as outcome. Furthermore, Experiment 2 shows that once goal-directed control has been established the dorsomedial prefrontal cortex is not directly involved in its maintenance but rather plays a central role in conflict resolution processes.

Keywords: instrumental learning, goal-directed action, response conflict, rats, prefrontal cortex

Goal-directed actions are highly flexible and can be controlled in the service of our current needs and desires. According to associative theory, goal-directed actions are mediated by a representation of the instrumental response-outcome contingency. The exact associative structure is subject to debate, but there is evidence to suggest that a representation of a goal or outcome (O) can activate the corresponding response (R) through an O→R association. According to the O-R theory of goal-directed action, these associations allow stimuli that make us think of the goals that we wish to pursue to activate the appropriate course of action via an S→O→R associative chain (Asratyan, 1965; Beritov, 1924; Elsner & Hommel, 2001; James, 1890; Pavlov, 1932; Trapold & Overmier, 1972). For example, when we are hungry, recalling a favorite cake can directly cause a trip to the local bakery, just as recalling a food pellet can elicit lever pressing by a rat trained with this reward (e.g., Balleine & Ostlund, 2007; Urcuioli, 2005). Our trip to get a cake from the bakery would, however, be fruitless at a time of day when the bakery is closed and should be inhibited in favor of, say, a trip to a late-night supermarket where we might have more success. Therefore, we need to be able to resolve conflict between competing goal-directed actions. The aim of the present experiments is to investigate the associative and neural mechanisms mediating this ability to resolve conflict in rats.

To this end, we trained rats on instrumental biconditional discriminations, which have previously been shown to lead to the formation of O→R associations (Kruse, Overmier, Konz, & Rokke, 1983). Our paradigm was, however, designed in such a way that O→R associations should evoke conflict. In our paradigm, the same events function both as discriminative stimuli, signaling which responses will be rewarded on each trial, and as the outcomes for correct responses. Response conflict should arise in an incongruent discrimination, in which the event that serves as the discriminative stimulus for the correct response in one component of the discrimination is the same as the event that serves as the outcome of the other correct response in the second component. For example, as illustrated in the top left panel of Figure 1, de Wit, Niry, Wariyar, Aitken, and Dickinson (2007) arranged for a lemon starch solution to signal that a press on a left lever by their rats yielded a coffee starch solution, and for the coffee solution to signal that a press on the right lever produced the lemon solution. Figure 1 (left bottom panel) also shows why O-R theory predicts that this discrimination should generate conflict. On trials starting with the lemon solution, this discriminative stimulus should come to activate a representation of the coffee outcome through an S→O association brought about by the Pavlovian relationship between the discriminative stimulus and outcome embedded within the instrumental contingencies in the discrimination. Activation of the coffee outcome representation should, in turn, elicit the correct response, the left lever press, through the O→R association. However, significant response conflict is induced because the lemon solution also serves as an outcome for the opposite response, the
right lever press, in the other component of the discrimination. The lemon solution should, as a consequence, not only indirectly activate the correct response via the representation of the coffee outcome but also directly activate the incorrect right lever press via an O→R association. The same conflict also arises in the other component of discrimination in which the coffee solution acts as the discriminative stimulus and the lemon solution as the outcome. Therefore, O-R theory predicts that the incongruent discrimination should be impossible to solve.

De Wit et al. (2007) compared performance of rats trained on an incongruent discrimination with that of rats trained on a congruent discrimination in which the discriminative stimulus and the outcome were always the same in each component of the discrimination; for example, as shown in the top right panel of Figure 1, for animals assigned to the congruent group, the lemon stimulus signaled that pressing the left lever would be rewarded with the lemon outcome, whereas the coffee stimulus signaled that right-hand lever presses would be rewarded with another drop of coffee solution. The associative structures that such training should engender, according to O-R theory, are again illustrated in Figure 1 (right bottom panel). Because each solution becomes associated with the same response in its dual roles as discriminative stimulus and as outcome, the rats need only learn the appropriate O→R associations; in this example, lemon→left lever and coffee→right lever associations. Therefore, the congruent discrimination does not produce any conflict and, in contrast to the incongruent, should be readily acquired.

At variance with the predictions of O-R theory, de Wit et al. (2007) failed to find a difference in the rate of acquisition of rats trained on the congruent and incongruent discriminations. What they did find, however, was that the two discriminations were mediated by different associative structures. To determine the role of O→R associations, following discrimination training they devalued one of the solutions by conditioning an aversion to it before assessing the rats’ propensity to perform the two responses in extinction and in the absence of the discriminative stimuli. The rationale for the devaluation test was straightforward. To the extent that responding is mediated by a representation of the outcome, devaluing the outcome should reduce performance of the corresponding response. Whereas responding following congruent training was susceptible to outcome devaluation, performance of the incongruent response was impervious to this treatment. The rats were just as likely to perform the incongruent response trained with the devalued outcome as the one trained with the still valued

\[ \text{Figure 1. Illustration of the incongruent and congruent discriminations (top right and left panels, respectively) and the associative structures that training on these discriminations should establish according to O-R theory (bottom panels). Starch solutions with coffee (C) and lemon (L) flavors served as the discriminative stimuli and outcomes; right and left lever presses were the responses (Rp and Lp). White and black arrows indicate correct and incorrect responses, respectively.} \]
outcome. Moreover, de Wit et al. (2007) observed exactly the same pattern of susceptibility to outcome devaluation for human participants trained on congruent and incongruent discriminations with visual icons acting as the stimuli and outcomes. The authors interpreted these results as evidence that the conflict engendered by O→R associations caused both rats and humans to solve the incongruent discrimination by acquiring direct S→R associations between the discriminative stimuli and the correct responses without encoding the natures of the outcomes.

Although the conflict engendered by the incongruent contingencies can be negated by pure S→R learning, there is evidence that rats, at least, can acquire an incongruent discrimination in a way that does encode the identity of the outcome. What appears to be important in determining the underlying associative structures is the nature of the foods used as stimuli and as outcomes. In contrast to the unidimensional flavored starch solutions employed by de Wit et al. (2007), Dickinson and de Wit (2003) used food pellets and a sugar solution, which differ both in their sensory properties (e.g., flavor) and motivational properties (with pellets being relevant to hunger only, while sucrose solution is relevant to thirst as well as hunger). Again, the rats were able to acquire the incongruent discrimination, and in fact, if anything, they learned it faster than the congruent discrimination. However, in this case devaluing either the pellets or sucrose by prefeeding to induce specific satiety selectively reduced performance of the response trained with the prefed outcome in both discriminations. This result suggests that, when food pellets and sugar solution serve as the stimuli and outcomes, the incongruent discrimination can be acquired successfully despite the formation of O→R associations.

In their analysis of goal-directed incongruent performance, de Wit, Dickinson and colleagues (de Wit et al., 2007; Dickinson & de Wit, 2003) noted that the incongruent discrimination should be insoluble in a goal-directed manner only if the encoding of a food as a discriminative stimulus and as the outcome overlap completely. Thus, differential encoding of a food in its role as discriminative stimulus and as outcome should allow the animal to acquire the incongruent discrimination. One potentially important respect in which discriminative stimuli and outcomes differ is when food is presented in relation to the time of response selection. Whereas the discriminative stimuli are present at the time of response selection, outcomes are at that moment in time merely anticipated. In associative terms, representations of the discriminative stimuli are activated directly by food presentations just before the opportunity to respond, whereas the outcome representations are activated associatively at the time of response selection and in this sense could be regarded as expected. It is therefore possible that the rats in the Dickinson and de Wit (2003) experiment solved the incongruent discrimination in a goal-directed manner by differentially encoding the foods in their roles as discriminative stimuli and as expected outcomes. Potentially, the differential sensory and motivational properties were used to form separate representations, for example, sensory stimulus and motivational outcome representations. In summary, there appear to be two possible strategies to solve the incongruent discrimination: an S→R habit strategy and a goal-directed strategy that involves differential encoding. In the present experiments, we aim to further investigate the latter strategy.

Experiment 1 assessed the possibility that foods may be differentially encoded by conducting a Pavlovian-instrumental transfer test following incongruent discrimination training. In Experiment 2, we investigated the effect of inhibiting the activity of the dorsomedial prefrontal cortex (dmPFC) on performance of the incongruent discrimination. We have previously reported that such inhibition selectively disrupts performance of the incongruent discrimination (de Wit, Kosaki, Balleine, & Dickinson, 2006), an effect that we interpreted in terms of the role of a conflict resolution process mediated by dmPFC. At issue in the present study was whether we could replicate this disruption in rats for which we demonstrated goal-directed incongruent performance in the first experiment and, if so, whether this disruption was accompanied by a loss of control over responding by O→R associations. An outcome-devaluation test was used to evaluate this hypothesis.

**Experiment 1**

Separate groups of food-deprived rats received incongruent and congruent training using the procedure employed by Dickinson and de Wit (2003). Each trial started with the delivery of either a food pellet or an aliquot of sucrose solution, followed by the insertion of two levers. Pressing one lever was rewarded on trials starting with the pellet stimulus, whereas the sucrose stimulus signaled that pressing the other lever would be rewarded. The discriminative stimulus and the rewarding outcome on a given trial were the same for the congruent group, but different for the incongruent group. Therefore, on incongruent trials with a pellet stimulus the outcome was the sucrose solution, whereas on the remaining incongruent trials the sucrose acted as the discriminative stimulus and the pellet as the outcome.

Following the acquisition of these discriminations, the role of O→R associations in the control of responding was assessed using a specific-satiety outcome devaluation test. In this test, the rats were prefed one of the two foods before the propensity to press the levers was assessed in extinction. To the extent that responding was mediated by a representation of the outcome, the rats should have performed the response previously rewarded by the prefed food less than that rewarded by the nonprefed food. Given that this procedure was similar to that used by Dickinson and de Wit (2003), we expected to replicate their findings: the rats should acquire the incongruent discrimination, if anything, more rapidly than the congruent discrimination and responding should be sensitive to outcome devaluation following both types of training. We then assessed the differential encoding of stimuli and outcomes by the incongruent group by giving Pavlovian conditioning outside the context of the discrimination training. During this conditioning, sucrose and pellets were each signaled by a different conditioned stimulus (CS; tone and noise) in the absence of the levers. During the subsequent transfer test, the levers were reinserted so that the rats had the opportunity to perform the discriminative responses in the presence of each of the CSs under extinction conditions. If the representation of the expected outcome was differentiated from that of the discriminative stimulus, we anticipated that a CS would bias responding toward the response with which it shared a common outcome. By contrast, if the stimuli and outcomes received common encoding during incongruent training we should not expect the presentation of the CS to systematically bias responding. During the final phase of the experiment, we confirmed that the actual presentation of the food pellet and
sucrose solution continued to exert stimulus control over instrumental performance in extinction.

In fact, a similar design was recently employed by Linwick and Overmier (2006). They trained pigeons on an incongruent discrimination in which “food” and “no-food” events acted as the discriminative stimuli and outcomes and then conducted a transfer test during which they presented CSs for the two types of events. In support of a differential encoding account, on average, the CSs biased responding toward the common outcome, although the bias was not statistically significant.

**Method**

**Subjects and Apparatus**

Sixteen female naïve Long Evans rats (Rattus norvegicus), approximately 2 months of age at the start of the experiment, were housed in pairs. Training and testing took place in 16 operant chambers (30 × 24 × 20 cm; Med Associates Inc, St. Albans, VT.) that were positioned in sound attenuating boxes. Chambers were illuminated by a 3-W, 24-V house light mounted on the top center of the wall opposite the magazine. A pellet dispenser and a syringe pump dipper could deliver 45-mg food pellets (BioServ, Frenchtown, NJ) and 0.1-ml sucrose solution (20% w/vol delivered over 2 s), respectively, to a recessed magazine (3.8 cm wide and 5.5 cm from the grid floor) situated in the center of the front wall. The boxes also contained a white-noise generator, a sonalert that delivered a 3-kHz tone, and a heavy-duty solenoid that could deliver a 5-Hz clicker sound. All stimuli were adjusted to ~85 dB. Sucrose delivery was always accompanied by the clicker sound to create a similar sound to that made by the pellet dispenser. An infrared photobeam positioned across the entrance to the food magazine allowed for the monitoring of magazine entries. Two retractable levers were placed on either side of the magazine. The levers were 4.8 cm wide and were positioned 17.5 cm apart and 9 cm from the grid floor. The apparatus was controlled and the data were collected by PC computers running the control language MED-PC (MED Associates Inc, St. Albans, VT).

Prefeeding before the devaluation tests took place in 16 plastic feeding-drinking boxes (40 × 20 × 20 cm). Pellets were presented in a glass bowl and the sucrose solution in an inverted 100-ml drinking cylinder.

**Procedure**

All animals were placed on a food deprivation schedule five days prior to training, and were maintained on this schedule by being fed ~15g of their maintenance diet each day following completion of the experimental sessions. Tap water was always freely available.

**Pretreaining.** Prior to pretraining, the animals were randomly assigned in equal numbers to either the congruent group or incongruent group. First, all rats received two sessions of magazine training, in each of which 15 presentations of sucrose solution and 15 presentations of food pellets were given randomly intermixed on a random time (RT) 60-s schedule with the levers withdrawn. In the next two sessions, the rats were trained to lever press to receive sucrose and pellets on a discrete-trial schedule. For half of the rats in each group, presses on the right and left levers were rewarded with the sucrose solution and pellets, respectively, with the remaining animals receiving the opposite correct lever-outcome assignment. Trials started with the insertion of one lever and the first lever press was rewarded with the appropriate reward. The first magazine entry after outcome delivery marked the end of the trial and caused the levers to retract. Trials were separated by an intertrial interval (ITI) that varied randomly between 5 and 30 s. Each session consisted of 15 trials with each lever, which were presented in random order. During the final two sessions of pretraining, responding was rewarded on a discrete-trial fixed interval (FI) schedule under which the first lever press that occurred 10 s after the insertion of the lever was rewarded. Throughout the experiment, a session began with the onset of the house light and terminated with its offset.

**Discrimination training.** During 12 sessions of discrimination training, half of the 30 trials started with the delivery of an aliquot of sucrose solution and half with the delivery of a pellet. These foods acted as discriminative stimuli signaling which lever press would be rewarded on that trial. Each rat was trained with the same lever press-outcome contingency as in pretraining. The first departure from the magazine after the delivery of a food stimulus led to the insertion of both levers. In the congruent group, the discriminative food signaled that lever presses rewarded with the same food type were correct, whereas presses rewarded with the different type of food were correct in the incongruent group. On each trial, responding on the correct lever was rewarded on the discrete-trial FI 10-s schedule, whereas responding on the incorrect lever was never rewarded and engaged a 2-s changeover delay. This delay reduced the fortuitous pairings of incorrect responses with reinforcement. The first magazine entry following reward delivery caused both levers to be retracted and initiated an ITI that varied randomly between 1 and 3 min. In all other respects, the procedure was the same as that employed during pretraining.

**Specific-satiety test.** Immediately following the last discrimination training session, all animals received their maintenance diet and tap water in the feeding-drinking boxes for a 1-hr familiarization period. On the next day, half of the animals in each group were given the opportunity to consume pellets for one hour in the feeding-drinking boxes, while the remaining rats received access to the sucrose solution. This prefeeding was followed by a 5-min extinction test, during which both levers were available, but responding was never rewarded. Sucrose solution and food pellets were not presented during this test, neither in their role of discriminative stimulus nor in that of outcome. The rats then received an instrumental discrimination retraining session before receiving a further devaluation test prior to which they were prefed the other food.

**Pavlovian conditioning.** During each of 16 sessions, two 2-min auditory CSs (tone and white noise) were each presented four times at variable intervals ranging between 2 and 6 min, with a mean of 4 min. Food pellets and sucrose solution were presented on an RT 20-s schedule throughout CS presentations. Half of the animals in each group received sucrose solution during the tone and food pellets during the noise, whereas the remaining rats received the opposite assignment. Two Pavlovian sessions were conducted on each day. During the first eight sessions, the order of trials and the duration of each ITI were pseudorandomly determined in each individual operant chamber, with the restriction that there were no more than two successive presentations of the same
During the following eight sessions, the CSs were presented in the same pseudorandom order in all chambers. Throughout each session, the levers remained retracted from the chamber.

**Pavlovian-instrumental transfer (PIT) test.** Following Pavlovian training, all rats received two retraining sessions on the discrimination schedule. On the next day, the first transfer test started with the insertion of both levers. Five minutes after the start of the session, 2-min presentations of the tone (T) and noise (N) were given in the following order: T-N-N-T-N-T-N. The ITI was fixed at 4 min, and lever pressing was recorded during the CSs as well as during the 2-min pre-CS intervals. After four presentations of each CS, the session ended with retraction of both levers. The following day, all animals received an identical transfer test, except for a reversal of the order of CSs. No food pellets or sucrose solution were delivered, as discriminative stimulus or outcome, during transfer testing.

**Reinstatement tests.** Subsequently, all rats received two Pavlovian retraining sessions. Over the next two days, each rat received four reinstatement tests, each of which assessed the effect of the presentation of a particular event: namely the tone, noise, sucrose, or pellet. Test sessions were presented in a fixed order: for half of the animals in each group, the order of tests was sucrose-noise-tone-pellet; for the remaining rats, the order of tests was tone-pellet-sucrose-noise. Each test started with 8 min of free access to both levers, after which one of the events was presented. Lever pressing was recorded during the 3 min preceding the events and during the 3 min immediately following offset of the 20-s CSs or following the first magazine entry after delivery of a food. Again, lever pressing was not reinforced with the food pellets and sucrose solution during this session so that responding was tested in extinction.

**Results**

The reliability of effects was assessed against a Type I error rate of 0.05, and the highest order interaction that is significant will be reported.

**Discrimination Training**

Discriminative performance was represented by a discrimination ratio, which was calculated by dividing the number of correct responses by the total number of responses during the fixed interval. Therefore, perfect discrimination yielded a ratio of 1 and nondiscriminative performance a ratio of 0.5. As shown in Figure 2, at the outset of training both groups were near chance, but over sessions discriminative performance improved, \( F(11, 154) = 27.66, \text{MSE} = 0.01 \). In contrast to the prediction of O-R theory, the incongruent group did not perform worse than the congruent group. In fact, the incongruent group exhibited superior discriminative performance, as demonstrated by a significant main effect of group, \( F(1, 14) = 8.12, \text{MSE} = 0.05 \).

**Specific-Satiety Test**

As can be seen in Figure 3, animals in both groups performed the response trained with the nonprefed outcome at a higher rate than the response trained with the prefed outcome. There was a significant main effect of prefeeding for these response rates, \( F(1, 14) = 21.84, \text{MSE} = 7.92 \), but the effect of prefeeding interacted with neither that of group, \( F < 1 \), nor that of the type of prefed food, \( F(1, 14) = 2.06 \). Preplanned separate analyses of the congruent and incongruent group showed that the effect of prefeeding was significant in each group, \( Fs(1, 7) = 11.21 \) and 10.67, \( \text{MSEs} = 7.48 \) and 8.35, respectively.

![Figure 2](image-url)  
*Figure 2.* Experiment 1: Discrimination training. Average discrimination ratios during 12 sessions of training for congruent (empty circles) and incongruent group (filled circles). Nonzero origin.
Pavlovian-Instrumental Transfer Test

To assess the effect of the CS presentations on instrumental performance, we computed the average number of responses per minute during the CS associated with pellets versus the CS associated with sucrose solution (collapsed across CS type; tone and noise) and during their respective pre-CS periods. We calculated separate scores for the first and second PIT test and for responses associated with the outcome signaled by the CS (common) versus responses associated with the opposite outcome (different). Finally, mean difference scores were calculated by subtracting the mean scores during their respective pre-CS periods from the mean numbers of responses during the CSs. The data of one animal in the incongruent group were excluded from analysis, because its difference score for correct responses minus that for incorrect responses (> 3 responses per minute) differed more than two standard deviations from the mean (0.5 responses per minute). An initial analysis on the number of responses per minute during the pre-CS period did not yield a significant effect of group, $F < 1$, with average response rates of 2.7 and 3.2 responses per minute in the congruent and incongruent groups, respectively. Neither was there a bias in baseline performance toward the response trained with the outcome signaled by the subsequent CS presentation nor a significant interaction between this transfer variable and that of group, $F < 1$. Therefore, we were justified in using the difference scores as a measure of transfer.

The CSs caused a relative enhancement of the response with which they had shared a common outcome with mean difference scores of 0.5 and 0.9 responses per minute in the congruent and incongruent group, respectively, when averaged across all CS presentations. In contrast, the response trained with the other food was not affected, with mean difference scores of -0.2 and 0.0 responses per minute in the congruent and incongruent group. There was a significant transfer effect, $F(1, 13) = 10.01, MSE = 1.64$, that interacted with neither the effect of group nor of food type, $F < 1$. Separate planned contrasts of the congruent and incongruent group were conducted because the critical prediction of O-R theory concerns the PIT effect in the incongruent group. However, although the transfer effect was reliable in the congruent group, $F(1, 7) = 6.74, MSE = 0.87$, it failed to meet the statistical criterion in the incongruent group, $F(1, 6) = 4.24, p = .09, MSE = 2.53$.

It is possible that the absence of a reliable transfer effect in the incongruent group was due to the impact of the extinction condition under which testing took place. To investigate this possibility, we conducted a separate analysis on the first CS presentation. Figure 4 depicts separately the difference scores of the congruent and incongruent groups collapsed across stimulus type. Analysis of the first stimulus presentation yielded a significant transfer effect, $F(1, 13) = 25.96, MSE = 2.02$, which again did not interact with group, $F(1, 13) = 1.02$, nor with food type, $F < 1$. Again, a separate analysis of the congruent group yielded a significant transfer effect, $F(1, 7) = 8.09, MSE = 2.23$, but it is important to note that this time the effect was also significant in the incongruent group, $F(1, 6) = 19.89, MSE = 1.78$, which indicated that the CSs biased responding toward the common outcome in this group.

Reinstatement Tests

Reinstatement was also assessed in terms of difference scores, which were calculated by subtracting the response rate during the 3 min preceding the event presentation from the rate during the 3 min following that presentation for the congruent group ($n = 8$) and incongruent group ($n = 7$) separately. The left panel of Figure 5 displays the difference scores separately for the responses that were correct (R+) and incorrect (R-) following the presentations of the food stimuli during training. The results of the CS-mediated reinstatement tests are shown in the right panel. In this case, response labels were based on the particular outcome signaled by the CS; R+ refers to the response that would have been correct were that outcome delivered whereas R- refers to the response that

![Figure 3. Experiment 1: Specific satiety test. Average number of responses per minute associated with the nonprefed (patterned bars) versus the prefed outcome (black bars) in the congruent and the incongruent group.](image)

![Figure 4. Experiment 1: Pavlovian-instrumental transfer test. Difference scores (responses per minute during stimulus minus during prestimulus period) for performance during the first stimulus presentation (collapsed across stimulus type and test), for the outcome signaled by the Pavlovian stimulus (patterned bars) versus for the different outcome (black bars). Difference scores of congruent ($n = 8$) and incongruent group ($n = 7$) are shown separately.](image)
would have been incorrect. The interpretation of these difference scores was not compromised by differences in the rate at which the correct and incorrect responses were performed prior to the presentation of the food stimuli. Neither the main effects of response, $F(1, 13) = 2.87$, and group, $F(1, 13) = 1.68$, nor the Group X Response interaction, $F < 1$, were significant. On average, the correct and incorrect responses were performed, respectively, at a rate of 0.4 and 0.5 lever presses per minute by the congruent group, and 0.9 and 0.8 by the incongruent group.

The results of primary interest concern the reinstating effects of foods in extinction, but we also included the results from the CS-mediated reinstatement tests in the analysis to rule out that the CSs exerted similar stimulus control as the foods with this procedure. This joint analysis did not yield a significant main effect of response, $F(1, 13) = 1.36$, $MSE = 1.93$, but a significant interaction between response and test, $F(1, 13) = 14.50$, $MSE = 1.60$, which prompted separate analyses of the food- and CS-mediated tests. We observed reinstatement of discriminative control by the foods in that the difference score was significantly greater for the correct response than for the incorrect one, $F(1, 13) = 10.85$, $MSE = 1.91$. This response effect did not interact with group or with food type, $F_5 < 1$. In contrast to the food stimuli, the CSs did not exert discriminative control. There was no significant overall response effect, $F(1, 13) = 1.77$, nor a Group X Response interaction, $F(1, 13) = 3.15$.

**Discussion**

Experiment 1 replicated our previous findings (Dickinson & de Wit, 2003) in two respects. First, rats can readily learn an incongruent discrimination, and indeed, the incongruent group acquired the discrimination more rapidly than the congruent group, a difference that was also observed by Dickinson & de Wit (2003) as a nonsignificant trend. A plausible explanation is that discriminative control by the foods in the congruent group was reduced as a result of negative priming, whereby representations that are already active are harder to reactivate and therefore form relatively weak associations. For example, Wagner’s (1981) SOP theory predicts that the consumption of a food pellet would function as a less effective outcome if preceded by the delivery of the same food pellets as a stimulus.

Second, to investigate the robustness of the outcome devaluation effect observed by Dickinson & de Wit (2003), we used a slightly different test procedure in which rats had the opportunity to perform both responses in the absence of the discriminative stimuli, thereby ensuring any devaluation effect was mediated by $O \rightarrow R$ associations. This same procedure was used previously to demonstrate that rats employ an $S \rightarrow R$ strategy to solve the incongruent discrimination when coffee and starch solutions act as the stimuli and outcomes (de Wit et al., 2007). In the present experiment, however, prefeeding a particular food selectively depressed the response trained with this food as the outcome in both the congruent and incongruent groups. This finding establishes that when pellets and sucrose, which differ in sensory as well as motivational properties, function as the stimuli and outcomes, responding after incongruent training is mediated by a representation of the outcome.

The novel finding was an outcome-specific PIT effect, with the presence of a CS selectively enhancing performance of the response with which it shared a common outcome following incongruent as well as congruent training. By contrast, actual presentation of the foods controlled responding in a way that reflected their stimulus function, a finding that accords with a study by Ostlund and Balleine (2007). Moreover, in the latter test context, there was no evidence that the CSs exerted any discriminative control over subsequent responding. This pattern of results accords with differential encoding of the foods in their roles of discriminative stimuli and outcomes, allowing the rats to solve the incongruent discrimination in a goal-directed manner.

**Experiment 2**

In a previous study, de Wit et al. (2006) demonstrated that the infusion of the GABA-agonist muscimol into the dmPFC selectively impaired performance of rats trained on an incongruent discrimination with the same outcomes, food pellets and sucrose.
solution, as used in Experiment 1. As GABA is the major inhibitory neurotransmitter, it is generally assumed that such infusions inhibit the normal neural activity in the target structure, thereby producing a temporary, reversible functional lesion. Given the claim that the dmPFC plays a role in conflict resolution in rats (Haddon & Killcross, 2005, 2006), de Wit et al. (2006) interpreted this finding as evidence that the solution of the incongruent discrimination depends upon the engagement of some form of conflict resolution process. However, the demonstration in Experiment 1 (see also Dickinson & de Wit, 2003) of goal-directed performance by the rats in the incongruent group, as assessed by outcome devaluation, raises an alternative account of the function of the dmPFC in these discriminations.

There is extensive evidence that instrumental performance of rats with lesions of the dmPFC is insensitive to outcome devaluation (Balleine & Dickinson, 1998; Corbit & Balleine, 2003), and therefore, it is possible that dysfunction in this area disrupts goal-directed control of associations between motivational outcome representations and the appropriate actions. Consequently, the purpose of the second experiment was not only to replicate the selective effect of dmPFC dysfunction on incongruent discriminative performance but also to assess the impact of such dysfunction on sensitivity to outcome devaluation. If the impairment of incongruent performance is produced by a loss of control over responding by O→R associations, we expect muscimol infusions in dmPFC not only to disrupt performance of the incongruent discrimination but also to reduce sensitivity to selective outcome devaluation.

Method

Subjects and Apparatus

The rats used in Experiment 1 remained assigned to their respective groups. The housing, deprivation, and testing conditions were identical to those reported in Experiment 1, except for single housing following surgery.

Procedure

Surgery. The animals were anesthetized with sodium pentobarbital (Nembutal; 1 mg/kg intraperitoneally), treated with atropine (0.05 ml), and then placed in a stereotaxic frame (Stoelting Co., Wood Dale, IL) with the skull positioned so that bregma and lambda were in the same horizontal plane. Small bilateral burr holes were drilled above the dmPFC of each hemisphere and three stainless steel screws were placed in the surrounding skull surface. Stainless steel guide cannulas (28 gauge; Plastics One Inc, Roanoke, VA) were implanted 1.5 mm above the target position (coordinates AP + 1.25, ML ± 0.75, DV −3.0) and secured to the screws with dental cement and covered with dust caps. One rat in the incongruent group did not recover from surgery. All animals were given a week to recover from surgery, during which they had free access to food, before being placed once again on the food-deprivation regime with water always freely available.

Infusion procedure. Infusions were made through 33 gauge internal cannulas, which protruded 1.5 mm below the tip of the guide cannulas. Either artificial cerebrospinal fluid (ACSF; 0.5 μl) or muscimol (0.5 μg dissolved in 0.5 μl ACSF; Sigma-Aldrich, St. Louis, MO) was injected into the left dmPFC at a rate of 0.5 μl per minute. The injectors were then kept in the same position for another minute. The same procedure was then applied to the right dmPFC. Following an additional 2 min, the rats were returned to the operant chambers for testing.

Tests of discriminative performance. Prior to testing, all animals received three retraining sessions using the original training programs. Before the first test, approximately half of the animals in each group (four animals in the congruent group and three in the incongruent group) received an infusion of muscimol, whereas the remaining animals in each group received an infusion of vehicle. The test session was identical to that used during discrimination training, except that it contained only four trials with each food stimulus, pellet (P) and sucrose (S), which were presented in the following order: P-S-S-P-S-P-P-S, and separated by an ITI fixed at 2 min. The following day, all animals were tested again, but no infusions were made. On the final day of testing, each animal received the other drug condition before being given a third test of discriminative control.

Specific-satiety test. Two subjects had to be excluded from the experiment because they lost their cannulas assemblies and one because of an error in the infusion procedure, leaving six animals in both the congruent and the incongruent group. Before testing, all animals received two retraining sessions on the discrimination schedule. The next day, half of the animals in each group were prefed sucrose solution and the other half food pellets immediately prior to receiving an infusion of either vehicle or muscimol (infusion protocol described above). Two minutes after the infusion, the animals received the opportunity to press both levers for 5 min in extinction. The following day, the rats received a retraining session on the discrimination schedule. The next day, each animal was prefed the same food but received the other drug condition. This allowed for a within-subject assessment of the effect of muscimol infusion into the dmPFC relative to that of vehicle infusion. Half of the animals in each group received a muscimol infusion on the first test and a vehicle infusion on the second test, whereas the remaining rats received the tests in the opposite order. In all other respects, the specific satiety tests were conducted in the same way as in Experiment 1.

Histological assessment. At the end of the experiment, all animals were anesthetized with Nembutal and perfused transcardially with phosphate buffered saline solution, followed by 4% formalin solution. The brains were stored in a 10% sucrose-formalin solution for at least 48 hr before 50 μm coronal sections were cut throughout the region of the dmPFC. Every other slice was stained with thionin, and the placement of the cannulas was examined by means of light microscopy.

Results

Histology

As mentioned above, two animals lost their cannulas assemblies and had to be killed prior to the implementation of the histological procedures. Histology was therefore performed on 13 out of the 15 animals that were tested. As can be seen in Figure 6, all cannula tips were localized in the anterior cingulate cortex (ACC) region of the dmPFC, predominantly in Cg2, but also in Cg1.
Tests of Discriminative Performance

There was no effect of stimulus food type on discriminative performance, $F(1, 13) = 3.85, MSE = 0.05$, with average ratios of 0.8 and 0.7 with the pellet and sucrose stimulus, respectively. As can be seen in Figure 7, discriminative performance differed during the three infusion tests. Whereas performance of the congruent and incongruent group was at a similar level following no infusion and vehicle infusion, performance of the incongruent group was selectively disrupted by muscimol infusion into the dmPFC. This conclusion was confirmed by statistical analysis. Although the Group X Test interaction just failed to reach the significance criterion, $F(2, 26) = 3.19, p = .06$, $MSE = 0.02$, separate preplanned analyses established that, whereas animals in the congruent group performed at indistinguishable levels during the three tests, $F < 1$, the discrimination ratios of the incongruent group varied with the type of infusion test, $F(2, 12) = 33.12$, $MSE = 0.01$. A post hoc analysis (Tukey-Kramer) showed that discriminative performance by the incongruent group was better following no infusion than following a vehicle infusion. It is more important to note, however, that the rats displayed an even greater impairment following infusion of muscimol relative to both the no infusion and vehicle infusion tests ($ps < 0.05$).

Specific-Satiety Test

The results of the specific-satiety tests following vehicle and muscimol infusion are displayed in Figure 8. An overall outcome devaluation effect was observed in that prefeeding a particular food reduced the performance of the response reinforced by that outcome during training relative to the rate of the other response, $F(1, 8) = 19.57$, $MSE = 0.43$. It is more important to note that neither the type of discrimination (incongruent vs. congruent) nor the type of prior infusion (muscimol vs. vehicle) significantly affected the magnitude of the devaluation effect, $Fs(1,8) < 1.13$, nor was there a significant interaction with prefed food type, $F(1, 8) = 4.51$. Moreover, separate preplanned analyses of the congruent and incongruent group both yielded a significant devaluation effect, with higher rates for the response trained with the nonprefed food than for that trained with the prefed food, $F(1, 4) = 10.80$ and $9.32$, $MSE = 0.59$ and 0.26, an effect that did not interact with infusion, $Fs < 1$. Therefore, inactivation of the dmPFC did not disrupt the associative structure mediating successful goal-directed action in the incongruent group.

Discussion

In Experiment 2, we replicated the previous demonstration that a treatment intended to inactivate the dmPFC disrupted performance of an established incongruent discrimination and extended the selectivity of this disruption from a comparison with a standard bidirectional control discrimination (de Wit et al., 2006) to a comparison with a congruent discrimination. Therefore, it seems that the dmPFC is not involved in the exertion of discriminative control in general, nor in the control by events that function not only as discriminative stimuli but also as outcomes (as in the congruent and the incongruent discriminations).

It is more important to note that within the present context, the muscimol infusion that produced deterioration in incongruent discriminative performance had no detectable impact on the sensitivity to outcome devaluation. Consequently, the deficit in congruent performance produced by dmPFC inactivation could not have resulted from a disruption of the goal-directed associative structure. We should therefore argue that this selective disruption reflects a dmPFC-based control process for resolving conflict between goal-directed actions in the incongruent discrimination. These results accord with and extend previous reports of a role of the rodent PFC in response conflict (Haddon & Killcross, 2005, 2006) and findings of conflict-related brain activity in the primate dmPFC (Botvinick, Cohen, & Carter, 2004; Haddon & Killcross, 2007) in tasks that involve conflict as a result of competing $S\rightarrow R$ associations.

General Discussion

The principal aim of our experiments was to investigate the processes that allow rats to resolve conflict between goal-directed actions caused by $O\rightarrow R$ associations. To this end, we employed the procedure of Dickinson and de Wit (2003) with pellets and sucrose solution as the discriminative stimuli and outcomes. First of all, we replicated our original finding that rats can acquire an incongruent discrimination and, if anything, do so more rapidly than a congruent discrimination (Dickinson & de Wit, 2003). This finding accords with a previous study showing that rats trained on an incongruent discrimination perform equally well as rats trained on a standard biconditional discrimination that should establish an equally complex associative structure without giving rise to conflicting $O\rightarrow R$ associations (de Wit et al., 2006).

The goal-directed nature of the responses trained under the present incongruent schedule was established by a significant outcome-devaluation effect in the incongruent group with rats responding less for a devalued than for a valued food in an extinction test (Experiment 1; see also Dickinson & de Wit, 2003). Moreover, a PIT test provided evidence that any conflict engendered by the goal-directed $S\rightarrow O\rightarrow R$ associative structure was minimized by the differential encoding of the sucrose solution and food pellets in their roles as discriminative stimuli and outcomes.

![Figure 6](image-url)  
*Figure 6. Experiment 2: Schematics of locations of tips of injection cannulas within the dmPFC (ACC: Cg1 and Cg2). Reprinted from The Rat Brain in Stereotaxic Coordinates (3rd ed.), by G. Paxinos and C. Watson, 1997. Copyright 1997.*
Earlier research investigated whether discriminative stimuli and outcomes could be differentially encoded on the basis of their locus in the trial structure but provided evidence against this possibility by demonstrating that the outcome of one trial functioned as an effective discriminative stimulus for the next trial (Dickinson & de Wit, 2003). The present study extended this research by investigating the possibility that the events could be differentially encoded because the discriminative stimuli, or at least their immediate after effects, were present at the time of response selection, whereas the outcomes were merely anticipated. We found that whereas pellets and sucrose solution continued to exert discriminative control in an extinction test, CS-elicited expectation of these foods enhanced performance of the opposite responses, namely those associated with these foods in their role of outcome. This result is the first evidence for the ability of rats to adopt a differential encoding strategy that gives rise to separate discriminative stimulus and outcome representations, thereby allowing them to solve the incongruent discrimination in a goal-directed manner.

As we noted in the introduction, it seems that this differential encoding strategy does not occur when starch solutions that only differ in flavor act as the stimuli and outcomes. De Wit et al. (2007) showed that under these circumstances rats prevented conflict by adopting a habitual $S \rightarrow R$ strategy. Similarly, human subjects trained with pictures of fruits also acquired habits to solve the incongruent discrimination (de Wit et al., 2007). These results suggest that the differential sensory (e.g., flavor and texture) and motivational properties of sucrose solution and pellets allowed for differential encoding of stimuli and outcomes in a way that the starch solution did not. For example, with sucrose and pellets, the discriminative stimuli may be encoded in terms of their sensory properties and the outcomes in terms of their motivational prop-

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**Figure 7.** Experiment 2: Infusion tests. Average discrimination ratios of congruent group (left panel) and incongruent group (right panel) after no infusion (dotted bars), muscimol infusion (black bars), or vehicle infusion (line-patterned bars). Nonzero origin.

**Figure 8.** Experiment 2: Specific satiety tests. Average number of responses per minute for the valued (patterned bars) versus for the devalued outcome (black bars), either following vehicle or muscimol infusion. Separate panels show performance of the congruent group (left panel) versus incongruent group (right panel).
erties. In accord with this analysis, Dickinson and Dawson (1987, 1989) showed that rats encode the relevance of the sucrose solution and/or the irrelevance of food pellets to the state of thirst during instrumental training under hunger. By contrast, the flavored starch solutions and fruit pictures used by de Wit et al. (2007) with rats and humans, respectively, would not support such differential motivational encoding. The rats and humans in de Wit et al.’s study (2007) were therefore forced to minimize conflict by acquisition of a simple S→R association that did not encode the identity of the outcome, thereby rendering responding insensitive to outcome devaluation.

The question remains whether or not differential encoding of the discriminative stimuli and outcomes provides a complete explanation of successful goal-directed acquisition of the incongruent discrimination, as it appears unlikely that differential encoding entirely eliminated response conflict. The discriminative stimuli and outcome events were physically identical events, and their representations would therefore be expected to overlap to a certain extent. The representation of the discriminative stimulus may not be purely sensory as the motivational properties of the stimulus food are experienced at the time of ingestion. On the other hand, satiety experiments provide good evidence for sensory encoding of outcome events, in that induction of sensory specific satiety for an outcome produces a reduction in the performance of a response trained with that outcome in a standard devaluation test (Balleine & Dickinson, 1998; Rescorla, 1990). Differential encoding may therefore need to be supplemented by an additional inhibitory process to entirely eliminate conflict in the incongruent discrimination.

We will now illustrate an associative account of incongruent performance that incorporates the differential encoding as well as an additional inhibitory process with an example. On trials when the sucrose solution acts as a discriminative stimulus signaling that right lever presses are rewarded with a food pellet, a predominantly sensory stimulus representation (Ss) should activate the correct right lever press via a predominantly motivational pellet outcome representation (Po). On the other trials, a sensory pellet representation (Ps) should activate the opposite response via the motivational sucrose representation (So). Some conflict should still arise, however, because the stimulus and outcome representations of each food are expected to share common elements. A possible mechanism for conflict resolution predicted by standard associative theory entails neutralization of response conflict by inhibitory S→R learning. For example, when the sucrose acts as the discriminative stimulus, it signals that left lever presses are nonreinforced. There is good evidence that such extinction can generate inhibitory S→R learning (e.g., Rescorla, 1993) so that an inhibitory association should be formed between the unique elements of the sensory stimulus representation of sucrose and the representation of the left lever press. This inhibitory association then serves to cancel any contribution of the motivational sucrose representation to response selection by the sucrose stimulus, so that the correct right lever press can be activated via an S→O→R associative chain incorporating the sensory sucrose representation and the motivational pellet representation. The corresponding structure is engaged when pellets act as the discriminative stimulus for the left press, which yields a sucrose outcome. In summary, in this associative model, inhibitory S→R associations allow for response selection to take place via S→O→R associative chains with separate sensory stimulus and motivational outcome representations.

What remains to be explained within this analysis is the role of the dmPFC in successful incongruent performance. Given that the disturbance of dmPFC function had no detectable effect on outcome devaluation, it is unlikely that the selective disruption of incongruent performance under muscimol reflected a loss of reward-guided action selection (e.g., Hadland, Rushworth, Gaffan, & Passingham, 2003; Rushworth, Walton, Kennerley, & Bannerman, 2004) or a failure to maintain activated goal-representations (e.g., Miller & Cohen, 2001). At first glance, these findings may seem inconsistent with an earlier demonstration that lesions of the prelimbic area of the dmPFC abolish sensitivity to outcome devaluation, but we should note that there are at least two possible reasons why the induction of dmPFC dysfunction had no impact of the sensitivity to outcome devaluation. The first relates to the specific locus of the dysfunction. Lesions that abolish sensitivity to outcome devaluation were located in the prelimbic area of the dmPFC (Balleine & Dickinson, 1998; Corbit & Balleine, 2003), whereas the cannula tips in the present study were restricted to the ACC region. The second reason relates to the stage of training at which the dysfunction was induced. Although prelimbic lesions prior to instrumental training render performance insensitive to outcome devaluation, Ostlund & Balleine (2005) have more recently shown that instrumental responding remains goal-directed when the prelimbic area is lesioned following instrumental training but prior to outcome devaluation. Consequently, even if the muscimol had spread from the cannula tips in the ACC to cause dysfunction in the prelimbic area in the present study, we should not necessarily have expected an impact on sensitivity to outcome devaluation.

At present, we can conceive of two possible functions for the dmPFC in the resolution of conflict in goal-directed incongruent performance. By appealing to dynamic filtering theory (Shimamura, 2000), de Wit et al. (2006) proposed that the dmPFC mediates the selective encoding of an event in its role of discriminative stimulus and outcome. As dynamic filter theory argues that one function of the dmPFC is to selectively allocate attention to task-relevant features in the face of conflict, it is possible that this area plays a central role in resolving conflict through the differential encoding of these events in terms of their sensory versus motivational properties. If the dmPFC supports differential encoding of the discriminative stimuli and outcomes in the incongruent discrimination, then dysfunction of the dmPFC should lead to response conflict.

Alternatively, the dmPFC may play a more general role in the resolution of conflict. In support of this possibility, Haddon and Killcross (2005, 2006, 2007) have reported that lesions of the dmPFC also disrupt performance on a conflict task that does not appear to involve differential encoding. In their task the dmPFC appears to play a role in the exertion of control by a contextual stimulus over appropriate responding in the presence of competing stimuli. One way in which the dmPFC could be involved in behavioral control by the discriminative stimuli in our task is through resolution of residual response conflict by suppressing inappropriate response tendencies via inhibitory S→R associations.

Whatever the specific nature of the conflict resolution process, our primary conclusions are twofold. First, when goal representa-
tions cause response conflict through O→R associations in an incongruent discrimination, rats are able to differentially encode present stimulus events and anticipated outcome events in order to allow for flexible goal-directed control. Second, the incongruent contingencies engage a conflict resolution process that is mediated by the dmPFC. Whether this conflict resolution process involves selective attention or inhibition of interfering responses elicited via O→R associations remains to be determined, but we have demonstrated that it does not involve the encoding of the action-outcome relationships that are necessary for goal-directed action. Therefore, once goal-directed actions have been acquired, the role of the dmPFC is to allow for behavioral flexibility by either recruiting or exerting directly the control required to resolve response conflict evoked by O→R associations.

References


