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Problem solving, inhibition and domain-specific experience: experiments on cottontop tamarins, *Saguinus oedipus*

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We present the results of experiments on cottontop tamarins designed to explore the relationship between problem solving, inhibitory control and domain-specific experience. The colony was divided into two groups: tool-experienced (TE) and tool-inexperienced (TI). The TE group had previously participated in a series of tool-use experiments and revealed that, when selecting a tool, they used featurally relevant dimensions (e.g. shape, material, orientation) over featurally irrelevant dimensions (e.g. colour). The TI group, although experienced in other laboratory-based experiments, had never been tested on tool or other object manipulation problems. In Phase 1, involving three conditions, all subjects were tested on a series of means–end problems involving the use of a cloth to access a piece of food. Although the correct choice always involved picking the supporting cloth, we also built in an association between the correct cloth and its colour. Once the subjects reached criterion, we reversed the association between the cloth colour and the food reward in Phase 2. If the subjects solved the problems in Phase 1 by attending to cloth colour, then in Phase 2 they should have difficulty, especially given prior findings on tamarins demonstrating that reversal learning is difficult. If the subjects solved Phase 1 by attending to the functionality of the problem (i.e. the physical/causal relationship between the cloth and food), then reversing the colours in Phase 2 should have no effect on the subjects' performances. Finally, if the subjects attended to both colour and functionality, then reversing the colours should cause some decrement in performance, but less so than in the case where colour alone dominates. In Phase 2, although both groups showed a decrement in performance, indicating problems with reversal learning, TE subjects significantly outperformed TI subjects. Furthermore, the pattern of performance for TE subjects suggested that they had solved the initial problem by attending to a combination of colour and functionality or functionality alone, while TI subjects had attended to colour alone. We conclude that for tamarins with experience as tool users, colour represents a less salient feature, even when it is systematically associated with a food reward. For inexperienced tamarins, however, colour is salient and reversal learning is difficult. Together, these findings highlight the importance of exploring the relationship between inhibitory control and domain-specific problem solving.

To survive, animals must discriminate among a variety of objects and events in the environment: some foods are toxic and some are edible; some heterospecifics are predators and some are prey; some conspecifics are dominant and some are subordinate. During the process of acquiring a discriminating palette, individuals must learn which features are relevant and which are irrelevant. In the classic ethological work on recognition systems, including studies of imprinting by Lorenz and aggression by Tinbergen, results showed that discrimination was often based on a simple feature, one tapping an innate releasing mechanism. Thus, young chickens imprint on the first moving object they detect, but show an initial bias to imprint on chicken-like things, especially if they have a head and eyes (Bateson 1966; Bolhuis 1991). Tinbergen's stickleback work showed that aggression could be released by a red belly, including that of the postman. If the initial discrimination is based on a feature that later turns out to be irrelevant or unreliable, then the individual must inhibit attention to this feature in favour of another with greater reliability. In the case of imprinting in chickens and aggression in sticklebacks, the underlying mechanism taps a statistical bias in the natural environment. In most cases, the first moving object detected by the chicken is its mother, and most red-bellied objects are stickleback competitors rather than postmen. Thus, in the natural world, chickens and

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sticklebacks are not confronted with the problem of inhibiting a previously formed association, and natural selection has favoured a domain-specific learning mechanism in each case.

Running in parallel to much of the work in ethology, both in the past and now, has been a comprehensive suite of experiments by comparative psychologists interested in the process of discrimination learning in animals (Herrnstein & Loveland 1964; Gallistel 1990; Herrnstein 1991; Thompson 1995; Shettleworth 1998). A central problem in this area, often referred to as the continuity–noncontinuity controversy (Spence 1940; Ehrenfreund 1948; Blum & Blum 1949), involves experiments where an animal first learns a discrimination between two objects (one object reinforced, the other not), and is then tested on a reversal-learning condition where the reinforcement contingencies are reversed. For example, consider a discrimination problem involving a positively reinforced black circle and a negatively reinforced white triangle. Whenever the subject selects the black circle, it receives food and whenever it selects the white triangle it receives a time out and no food. With respect to discrimination, subjects might use colour, shape, or a combination of colour and shape. If subjects use only one featural dimension, then reversal learning is expected to be more difficult than if subjects use a combination of features. The reason for this is that with one feature, the strength of the association between feature and reward is stronger. Carrying this logic through, if the transfer task involves a change of reinforcement from black circle to white triangle, then subjects using colour alone will have difficulty learning this new discrimination because it forces them to inhibit the previously learned association between black and positive reinforcement; the same prediction holds for subjects focusing on shape in the initial condition. In contrast, if the transfer task involves a change in reinforcement from black circle to black triangle, then performance should remain steady for those focusing on colour alone, because black is still positively associated with reinforcement. Finally, if subjects solve the initial discrimination task by extracting both black and triangle as relevant features, then their performance on the reversal problem will be better than subjects attending to colour or shape alone.

Two questions arise from this testing situation. What feature or features does the animal extract in order to solve the discrimination, and what difficulties does it encounter during reversal learning? As much of this literature has demonstrated, the patterns of responses are influenced by initial attentional and biological biases that cause some features of some stimuli (e.g. food, water, shock, lights) to be more salient than others (Garcia & Koelling 1966; Mackintosh 1977; Gillette et al. 1980).

In an elegant, and recent comparative analysis, Rumbaugh (1997) used the problem of reversal learning to explore both species differences in inhibitory control among primates, as well as the relationship between brain size and discrimination learning. In the initial task, subjects were trained to discriminate between a reinforced and a nonreinforced abstract object or geometric shape until they reached criterion. The reversal trials that followed consisted of three conditions in which the subjects had to inhibit their preference for the object/cue that was reinforced in the initial task, selecting instead either the previously nonreinforced object/cue or the novel object/cue, depending on the condition.

Based on the comparative data, Rumbaugh (1997, page 24) concluded that the 'smaller-brained primates' performance indicated that they were basic stimulus-habit learners. By contrast, the apes found all test conditions equally easy'. Although some general differences do emerge between the great apes and the other nonhuman primates, the patterns are not as straightforward as indicated. In particular, the only consistent pattern is that the overall level of performance on each condition was higher for all apes by the second trial. On the first reversal trial involving a novel object/cue and an object/cue that changed from nonreinforced to reinforced, rhesus monkeys, *Macaca mulatta*, outperformed (accuracy of 70%) all of the apes whose accuracy scores ranged from 10% (gibbons) to 45% (gorillas); rhesus continued to improve over the session, and ended with scores equivalent to the apes, including those considered 'bright' and language-trained by Rumbaugh. This shows that apes have greater difficulty with the described reversal problem (i.e. ignore the new object/cue, pick the previously nonreinforced object/cue) than with the other conditions, and that a straightforward relationship between brain size and reversal learning is violated by the rhesus monkey results. Furthermore, there were no consistent patterns among the lemurs, New and Old World monkeys. Thus, for example, squirrel monkeys showed no consistent differences across reversal conditions, while lemurs showed completely inconsistent patterns throughout the session. In general then, most primates appear to have difficulty with reversal learning, a difficulty that reflects upon their capacity for inhibitory control (Diamond & Goldman-Rakic 1989; Diamond et al. 1989; Diamond 1990; Dias et al. 1996a, b; Roberts et al. 1998; Hauser 1999; Roberts & Wallis 2000).

The strength of ethological studies of discrimination learning is that they tap species-typical behaviour, focusing on different domains of learning. Thus, ethologists ask whether the features used to discriminate objects in one domain differ from those used in other domains. Support for this perspective comes from studies of landmark use in spatial navigation, object selection in tool use, and food choice (for reviews, see Shettleworth 1998; Hauser 2000; Santos et al. 2001, in press). The strength of comparative psychological experiments on discrimination learning is that they are based on tightly controlled experiments that clearly articulate the underlying mechanisms (reviewed in Roberts 1998). Thus, comparative psychologists have demonstrated why some reversal learning problems are more difficult than others, and in some cases, why some species may perform differently (Lawrence 1950; Kendler et al. 1961; de Lillo & Visalberghi 1994; Rumbaugh 1997). One contribution to this problem, then, would be to devise experiments that tap the strengths of each of these disciplines. In this paper, we explore the problem of discrimination learning in cottontop tamarins and attempt to address three

Table 1. Subjects' family, sex, training association colour, prior experience with tools as well as with other laboratory experiments

Subject	Sex	Family	Training group	Training association*	Experience with tool experiments†	Experience with other experiments†
ID	M	Family 2	Experienced	Blue	1	2, 3, 4, 5, 6, 7, 8
EN	F	Family 3	Experienced	Blue	1	3, 5, 6, 7, 8
PB	M	Family 2	Experienced	Red	1	3, 5, 8
KW	F	Family 2	Experienced	Red	1	5, 7, 8
ES	F	Family 1	Inexperienced	Blue	None	2, 3, 4, 5, 6, 7, 8
DD	M	Family 1	Inexperienced	Blue	None	2, 3, 5, 6, 7, 8
SH	F	Family 4	Inexperienced	Red	None	3, 5, 6, 7, 8
RW	M	Family 4	Inexperienced	Red	None	3, 4, 5, 6, 7, 8
RB	F	Family 1	Inexperienced	Red	None	3, 4, 5, 6, 7, 8

*Half of the subjects were presented with a correct (i.e. reinforced with food) blue cloth and half with a correct red cloth.

†1=L. R. Santos, H. E. Pearson, G. M. Spaepen & M. D. Hauser (unpublished data): a tool (means)–food (end) manipulation task completed 1 week before the present study; 2=Santos et al. (1999): an inhibition reaching task for food completed 4 years before present study; 3=L. R. Santos, C. T. Miller & M. D. Hauser (unpublished data): expectancy violation study involving passive, unreinforced viewing of artefact-like objects completed 2 years before present study; 4=Hauser et al. (2001): object knowledge task involving active manipulation of apparatus doors for food reinforcement completed 1 year before present study; 5=Ramus et al. (2000): habituation–discrimination task involving passive, unreinforced listening to speech stimuli completed 1 year before present study; 6=Deipolyi et al. (2001): searching task involving the use of differently coloured and shaped landmarks associated with food, completed 6 months before present study; 7=Ghazanfar et al. (2001): task involving passive, unreinforced listening to conspecific vocalizations followed by the production or suppression of an antiphonal response, completed 6 months before present study; 8=Kralik et al. (2002) reversed contingency task involving reaching for different food quantities, completed 1 year before the present study.

questions. First, when tamarins solve a discrimination problem, are some features more salient than others, and if so, why? Second, given the features attended to in the initial discrimination, how much difficulty do tamarins have in learning a new discrimination when the association between discriminative feature and reinforcement is reversed? Third, does domain-specific expertise on a problem change the process of reversal learning, and consequently, of inhibitory control?

Several factors guided our choice of species and discrimination problems. We selected cottontop tamarins as subjects because we already have a considerable understanding of how they discriminate objects from different domains (e.g. tools: Hauser 1997; Hauser et al. 1999; number: Uller et al. 2001; space: Deipolyi et al. 2001; faces: Weiss et al. 2001; abstract relationships between two-dimensional images: Kralik & Hauser 2002; trajectories of invisibly displaced objects: Hood et al. 1999; Hauser et al. 2001). Furthermore, several studies have explored the tamarins' capacity for inhibitory control, revealing a number of circumstances where learning to solve a problem is greatly delayed or blocked by difficulties associated with inhibition (Hauser 1999; Hauser et al. 1999, 2001; Hood et al. 1999; Santos et al. 1999; Kralik et al. 2002). Our discrimination problem, a means–end task involving the use of a tool to gain access to food, has already been tested on one group of tamarins, and reveals important information about their preferential use of some features over others. Specifically, based on two sets of experiments (Hauser 1997; Hauser et al. 1999), tamarins appear to treat information about shape and material as dominant features when selecting an appropriate tool, while treating such features as colour as relatively subordinate or insignificant. Thus, for example, if a blue cane has proven effective as a tool for acquiring food, then tamarins readily transfer this knowledge to differently coloured canes, but not necessarily to differently shaped objects. In this paper, we leave open the question of whether the tamarins' performance is primarily mediated by perceptual or physical/causal aspects of the task (Hauser 2001; Povinelli 2001).

METHODS

Subjects

We tested nine cottontop tamarins from the Primate Cognitive Neuroscience Laboratory at Harvard University. All our subjects were born in captivity and tested as adults. Subjects were fed a diet of marmoset chow, mealworms, crickets, fruits, yogurt, sunflower seeds and peanuts, and were provided with ad libitum access to water. Supplementary food was provided during experiments, including raisins, Froot Loops and marshmallows. Our subjects lived in social groups consisting of a breeding pair, and in some cases one to two generations of offspring. For testing, we removed subjects from their home room cage by luring them into a transport box with a raisin or marshmallow. We only removed subjects from their home cage if they left voluntarily.

Table 1 presents data on each subject's family membership, sex, initial training group and experience with tools as well other laboratory experiments. Although all subjects had been tested in prior experiments, and some involved the use of colour in discrimination (e.g. Deipolyi and colleagues' (2001) landmark spatial task), only four of the nine subjects (Table 1) had any experience in experiments involving the use of tools to gain access to food. These subjects comprised the tool-experienced (TE) group. Several weeks before the present experiments, the TE group was run on a series of experiments involving the use of objects to gain access to food. Specifically, all of the subjects started with a training phase involving the use of a blue cane to obtain a piece of marshmallow out of reach (Hauser 1997). In this initial condition, the marshmallow was either inside the hooked portion of the cane or outside of it. Once the tamarins reached criterion, pulling the cane with a marshmallow located inside the hook, we tested them on a suite of generalization conditions involving featural changes (e.g. colour, shape, size and material of the object), as well as physical/causal properties of the task (e.g. problems involving traps, broken canes and rakes with the tines down versus up). Relevant to the current experiments, the subjects treated material and shape as the dominant features in the discrimination, while treating colour as relatively subordinate or irrelevant (Hauser 1997; unpublished data). Thus, although the tamarins were trained using a blue cane, they readily transferred to canes of a different colour, but not to canes with functionally inappropriate shapes or made of functionally inappropriate material (e.g. rope). Of most direct relevance to the present experiment, therefore, when tamarins acquire skills as tool users, they apparently weight functionally relevant features such as the relationship between shape and the location of the reward as highly salient, and features such as colour as either less salient or irrelevant to the task. Importantly, tamarins do not ignore colour in all tasks as evidenced by studies of landmark use (Deipolyi et al. 2001).

Subjects without experience using tools (tool-inexperienced: TI group) did, however, have other experimental experience (see Table 1). Specifically, like the TE group, they had previously been tested with a reaching experiment (Santos et al. 1999), a passive viewing experiment in which they had to discriminate the shapes and colours of functional objects (L. R. Santos, C. T. Miller & M. D. Hauser, unpublished data), an object knowledge search task in which they manipulated doors to gain access to food (Hauser et al. 2001), a spatial foraging experiment in which subjects used the colour, shape and orientation of objects to locate hidden food (Deipolyi et al. 2001), as well as a number of acoustic discrimination tasks (Ramus et al. 2000; Ghazanfar et al. 2001). Thus, although TI subjects had no experience manipulating tools, they all had considerable experience in other experiments.

Experimental Procedure

The primary task involved using a piece of cloth to retrieve a piece of food placed out of reach. This task has been used before with another group of tamarins (Hauser et al. 1999). In brief, while the subjects sat in a Plexiglas test box, we presented them with a tray divided into two sides by a barrier. On each side of the barrier, we placed a piece of cloth (for dimensions and configurations, see Hauser et al. 1999). On each trial, there was no more than one correct choice. A correct choice was defined as that piece of cloth which, when pulled by the tamarin, brought the marshmallow within reach. Thus, for example, pulling a piece of cloth that made no contact with the marshmallow was incorrect, and so was pulling a piece of cloth that was clearly disconnected from a second piece of cloth above it that supported the marshmallow. The primary difference between the task presented in Hauser et al. (1999) and the one presented here is that in the current version, the physically correct solution was also associated with a cloth of a particular colour. Thus, subjects could solve the problem by choosing to attend to one or both of the key discriminating features: the cloth colour and the physical/causal connection between cloth and marshmallow.

In each session, for each of the conditions described below, we ran 20 trials. We counterbalanced the order of the presentation of the trial type within the session, but all the sessions consisted of 10 correct trials on the right and 10 correct trials on the left. To advance to the next condition, we required all the subjects to obtain accuracy scores of 18 out of 20 or better on two consecutive sessions.

Phase 1 involved three conditions, each designed to illuminate possible differences in learning curves between TE and TI subjects. We started all subjects on Condition A (see Fig. 1). Condition A mirrored the first training condition of Hauser et al. (1999) and involved manipulations of the food position relative to a continuous piece of cloth, with the correct choices involving pieces of marshmallow on the cloth, and incorrect choices involving pieces of marshmallow off the cloth. The subjects could solve this problem by attending to the physical/causal connection (On versus Off), colour (Blue versus Red), or a combination of these two dimensions. As indicated in Table 1, some subjects were rewarded for picking the blue cloth and some for picking the red cloth. Thus, for example, subjects tested on Blue/R+ could solve the problem by simply picking the blue cloth on every trial, independent of the food position. In contrast, subjects attending to the physical/causal relationship between food and cloth, would have to pick the cloth supporting the food in order to obtain it.

Condition B preserved the colour association of Condition A, but added on a new physical/causal relation: although some pieces of cloth supported the food, they were disconnected from the second piece of cloth, which was too far to reach (Fig. 1; Hauser et al. 1999). As in Condition A, colour provided a perfect predictor of reinforcement, and thus, could be used to select the connected piece of cloth independently of any understanding of the physical/causal problem. If the subjects learned to use colour to predict reinforcement in Condition A, then when tested on Condition B, they should show little or no decrement in performance since colour continues to be perfectly correlated with reinforcement. In contrast, if subjects learned to use physical/causal relations to predict reinforcement in Condition A, then in moving to a slightly different problem in

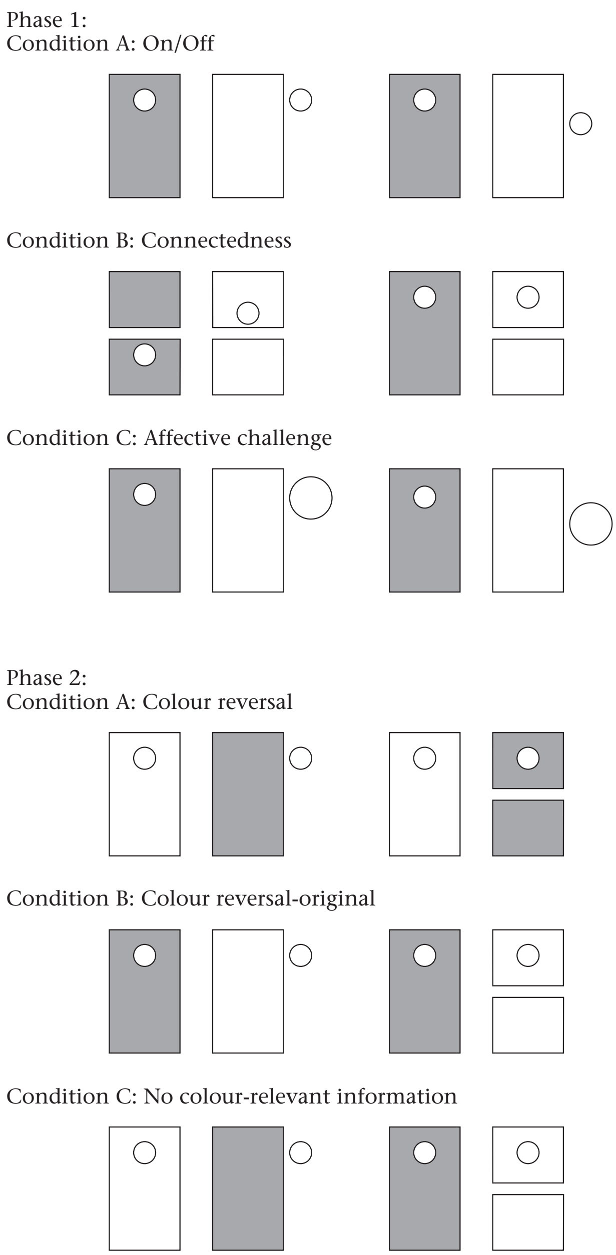

Figure 1. An example of a subset of trials per phase and condition. Here, we illustrate two trials per condition for subjects starting with Blue cloth=R+ (□), Red cloth=R− (□). Cloths are represented by rectangles and food reinforcement (R) as white circles. Within each session and condition, subjects received an equal number of correct trials on the right and on the left.

Condition B, they should show a decrement in performance. This is what Hauser et al. (1999) found in their initial report on this task. Having reached criterion on Condition B, the subjects moved on to Condition C. Once again, the colour–reward association set up in Condition A was preserved, but a motivational or affective challenge was presented: although both colour and physical/causal factors still predicted reinforcement, a larger piece of marshmallow was associated with the incorrect cloth (see Fig. 1). This condition was set up as an inhibitory challenge, testing both subjects who learned the discrimination on the basis of physical/causal factors, colour, or both. If the subjects learned that the physical/causal connection between cloth and food, or the colour of the cloth, predicts reward, then they should reject the cloth associated with the larger piece of marshmallow. Our previous experiments showed that tamarins have difficulty inhibiting the prepotent motivation to reach for the larger, but unattainable, marshmallow piece, even when they demonstrate competence with the general means–end task (Hauser et al. 1999).

Phase 2 focused on reversal learning, and involved three conditions. Condition A presented a combination of the physical/causal problems (i.e. On/Off and Connectedness) conducted in Phase 1A and B, but reversed the colour–reinforcement associations (see Fig. 1). Thus, for example, subjects tested on Blue/R+, Red/R − in Phase 1 were tested on Blue/R − , Red/R+ in Phase 2. Once subjects reached criterion, they were tested on Condition B, which again reversed the colour-reinforcement associations. Thus, subjects were tested on the colour–reinforcement association they had originally been trained on (see Fig. 1). The purpose of this condition was to investigate whether or not subjects would be able to switch back after the original reversal. Lastly, we tested subjects on Condition C (see Fig. 1) involving no colour-relevant associations. Thus, we presented both blue and red cloths, but colour no longer predicted the correct solution. Specifically, both red and blue cloths were associated with pieces of food on and off the cloth within a trial.

Predictions

Given the literature on discrimination learning in animals, we generated the following predictions. First, if TE subjects learned to use one object to obtain another, then they should perform better on Conditions A and B of Phase 1; TI subjects may perform as well as TE subjects on Condition B if they learned to attend to colour, ignoring all other aspects of the task. TE subjects might also be expected to perform better than TI subjects on Condition C if their overall level of expertise provides them with better inhibitory control in the face of an affective challenge. Second, if TE subjects learned to ignore colour as a relevant feature, but attended to physical/causal properties, then in Condition A of Phase 2, they should also show little decrement in performance relative to TI subjects. More specifically, TE subjects should be less likely to use colour to solve the discrimination problem in Phase 1, and thus, should not be affected by colour reversal because colour plays no role in the solution. In contrast, if TI subjects solved the initial discrimination problem by using colour, the simplest and perhaps most salient feature, then they should have great difficulty with Condition A of Phase 2. An alternate possibility was that subjects in either or both groups would attend to a combination of colour and physical/causal features, and consequently, show some decrement in performance on the first few trials of the reversal condition. The relevant analysis would then involve a contrast in learning curves between TE and TI subjects.

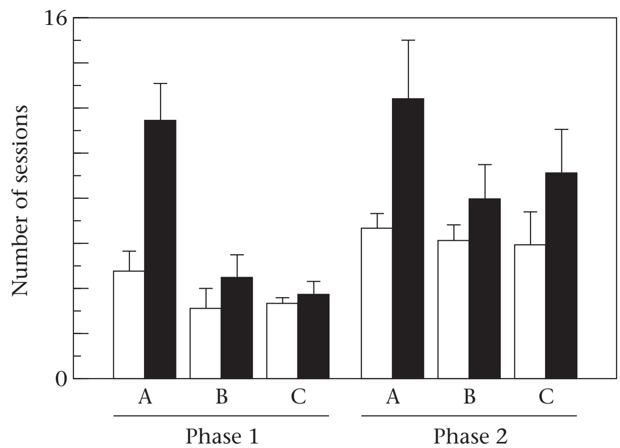

Figure 2. Number of sessions required to reach criterion (two sessions with accuracy scores of 18/20 or better) on each condition, contrasting performance by tool-experienced (□) and tool-inexperienced (■) subjects. Mean+SE are presented.

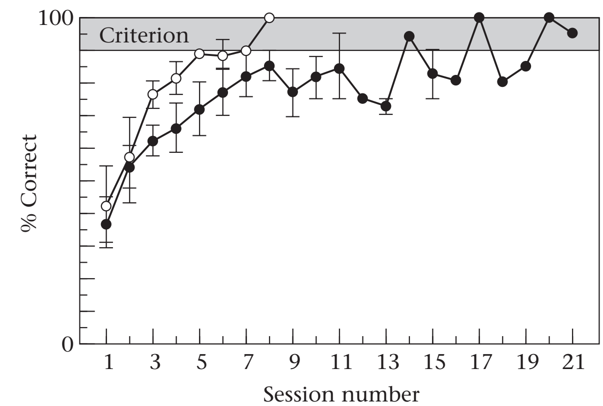

Figure 3. Performance (percentage correct by session) on the first reversal condition (2A) as a function of experience with tools (○=tool experienced group; ●=tool-inexperienced group). Mean±SE are plotted for each group.

RESULTS

Figure 2 depicts the mean number of sessions needed to reach criterion across all conditions for subjects in the TE and TI groups. We entered these data into an analysis of variance (ANOVA) with group (TE and TI) as a between-subjects factor and condition (1A, 1B, 1C, 2A, 2B, 2C) as a within-subjects factor. We found a main effect of group ($F_{1,7}$=9.84, P=0.017). Across all conditions, TE subjects reached criterion faster than TI subjects. We also found a main effect of condition ($F_{5,35}$=6.06, P=0.0004). As Fig. 2 illustrates, both groups took longest in Condition 1A, the original learning condition, and Condition 2A, the initial reversal condition. We also examined the interaction between group and condition. Although this omnibus interaction did not reach statistical significance ($F_{5,35}$=1.66, P=0.17), we decided to explore more focused comparisons within condition using nonparametric Mann–Whitney analyses. We chose the Mann–Whitney test because it evaluates the rank order of sessions to criterion by group and is thus preferred for smaller samples sizes. The only statistically significant differences across groups occurred in Conditions 1A and 2A. In Condition 1A, the original training condition, TE subjects reached criteria faster ($\bar{X} \pm$ SD=4.8 ± 1.7 sessions) than TI subjects (11.4 ± 3.6 sessions; Mann-Whitney U test: U=1.0, N_1=4, N_2=5, P=0.03). In Condition 2A, the first reversal condition, TI subjects took longer to reach criteria (12.2 ± 5.8 sessions) than TE subjects (6.5 ± 1.3 sessions; U=2.0, N_1=4, N_2=5, P=0.05).

To examine further the difference in reversal learning across the two groups, we investigated subjects' performance on the first trial of the reversal condition, Condition 2A. TE subjects performed no better on their first reversal session ($\bar{X} \pm$ SD=43 ± 0.24% correct) than TI subjects (37 ± 0.18% correct; U=4·6, N_1=4, N_2=5, P=0.70). To examine differences in performance over time, we computed a multiple regression with session number and group as factors. We found that TE subjects had a steeper learning curve than TI subjects (unpaired t test: t_7=4.57, P=0.0001; see Fig. 3). In other words, TI subjects learned the reversal condition at a slower rate than TE subjects, but this pattern was only significant for the first of the Phase 2 reversal conditions.

Although our samples sizes are small, the design of our experiment allowed us to set up explicit predictions with respect to how each feature associated with the task potentially contributed to the subjects' performance. In Fig. 4a, we plot the predicted effects on performance, contrasting the number of sessions to criterion on 1C (i.e. the final condition in Phase 1) with the number of sessions to criterion on 2A (i.e. the first reversal condition of Phase 2); this was a relevant contrast because there was no statistically significant difference in performance between TE and TI subjects in Condition 1C. If subjects solved Phase 1 by attending to colour alone, then such individuals should show the greatest decrement in performance (i.e. the largest increase in the number of sessions to criterion) in 2A. In contrast, if subjects attended to the physical/causal properties of the task alone, they should show no change in performance between 1C and 2A. Finally, if subjects attended to both colour and physical/causal properties of the problem, they should show an intermediate response.

Figure 4b plots the results for each subject, divided into tool-experienced and tool-inexperienced subjects. Although we are unable to explore these patterns quantitatively, we can make two general points. First, most subjects appear to have attended to colour as a predictive feature in Phase 1, as evidenced by the increasing slopes shown by both TE and TI individuals. Second, most of the TE subjects showed flatter slopes than TI subjects, and for subjects EN and PB in particular, the relative contribution of colour appeared to be insignificant, as indicated by the flat slope from 1C to 2A.

DISCUSSION

The aim of our experiments was to explore the relationship between problem solving, inhibitory control and domain-specific experience. Here, we evaluate our results

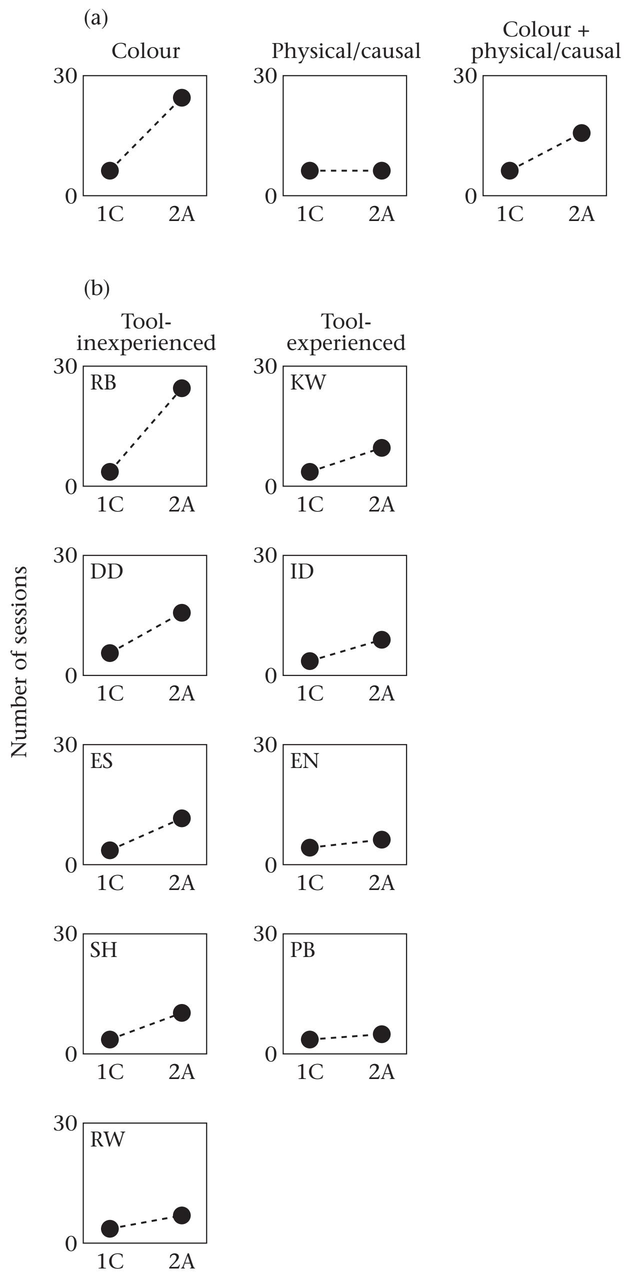

Figure 4. (a) Hypothetical patterns of performance based on the feature or features used to solve Phase 1. Hypothetical data are plotted for the number of sessions to reach criterion on 1C (the final condition with one colour associated with reinforcement) and 2A (the first colour-reversal condition). (b) Individual patterns of performance (number of sessions to criterion) for 1C and 2A, contrasting tool-inexperienced subjects with tool-experienced subjects; subject identifications indicated in upper left-hand corner.

in light of these issues, and in particular, the three questions raised in the Introduction.

First, when tamarins solve a discrimination problem, are some features more salient than others, and if so, why? Each experimental condition presented a variety of potentially significant features with regard to solving the discrimination problem, including most importantly cloth colour and physical support of the food by a continuous piece of cloth. As in earlier studies of the continuity–noncontinuity problem as the role of selective attention to particular features (Spence 1940; Ehrenfreund 1948; Mackintosh 1977), our goal was to determine which feature or features are salient. In Condition 1A, TE subjects solved the discrimination problem faster than TI subjects. There are several possible interpretations of this difference in performance. For example, TE subjects may have solved the problem faster simply because they had more experience (domain-general) with means–end problem solving and/or object manipulation. Alternatively, they may have solved the problem faster because of greater domain-specific experience that caused them to focus on the causal/physical features of the problem. Finally, it is possible that because TE subjects had more experience in object-manipulation tasks, they picked up on the association between colour and reward more rapidly.

Depending upon each subject's strategy for solving Condition 1A, Condition 1B either presented a new problem or precisely the same one. If subjects solved Condition 1A by attending to the position of the food on or off the cloth, then Condition 1B provided a new relational problem, one requiring attention to the connectedness of the cloths as well as the relative placement of the food. In contrast, if subjects solved Condition 1A by attending to colour, then Condition 1B presented the same colour–reward association. If subjects used a combination of physical support and colour to solve 1A, then they would have to learn the new support problem in 1B, but would be able to use colour as a reliable predictor of reward. Although we found no statistically significant difference in performance between groups, TI subjects showed a greater improvement in performance from Condition 1A to 1B, whereas TE subjects did not. This difference in performance between groups can be explained in two ways. First, by the time individuals solve the initial On–Off problem (Condition 1A), independently of prior experience, they can generalize to the problem of connectedness, either because of the perceptual similarity between tasks or because of their understanding of the more general problem of physical support. Second, if TI and/or TE subjects used colour to solve 1A, then in 1B, colour would have been as good a predictor of reinforcement; consequently, subjects should have reached criterion quickly on 1B. In our earlier work (Hauser et al. 1999), subjects starting with the On–Off condition did not readily transfer to Connectedness, suggesting that these were perceived as different physical/causal problems. This result, considered in the context of the present experiment, suggests that both TE and TI subjects attended to colour, thereby facilitating the transfer from one physical/causal task (i.e. On/Off) to a second (i.e. Connectedness). As Povinelli (2001) correctly points out, this initial transfer does not show that subjects understand the physical/causal problem. Additional conditions must be run, including some of the manipulations that have been previously run on tamarins and chimpanzees, *Pan troglodytes*. Our concern in the experiments presented here, however, was not with the distinction between physical/causal understanding as opposed to simpler perceptual generalizations. Rather, Condition 1B was run to determine whether prior experience, either from prior experiments (i.e. TE subjects), or from Condition 1A more specifically, would facilitate reaching criterion on this new task. For TI subjects, prior experience with Condition 1A clearly influenced performance. For TE subjects, prior experience failed to show a detectable effect on performance. One possible explanation for this result is that TE subjects were at ceiling with respect to their performance on this task; additional experiments are needed to test between these interpretations.

Condition 1C asked whether subjects in both groups could handle an affective challenge, one involving inhibitory control over the presumed motivation to reach for a larger (unattainable) piece of food over a smaller (attainable) one. Although there was no difference in performance between groups, there was also no difference in performance between Conditions 1B and 1C. Thus, independently of experience, and the feature or features used to solve this means–end task, subjects in both groups were able to inhibit the affective challenge presented. These results also stand in contrast to previous findings (Hauser et al. 1999) where subjects initially reached for the cloth associated with a large but inaccessible piece of food as opposed to a small but accessible piece of food. This suggests that in the present experiments, the addition of colour as a perfectly predictive feature associated with reinforcement made it easier for the tamarins to inhibit their motivation to reach for the larger, but unattainable, piece of food.

Phase 2 was designed to show both which feature or features were used to solve the initial discrimination problems in Phase 1, and to assess the degree of inhibitory control. As articulated in the Introduction, we predicted that if subjects attend to colour in solving the problems in Phase 1, then they would show the greatest decrement in performance in Phase 2. In Condition 2A, TI subjects showed an approximately two-fold increase in the number of sessions to criterion relative to their performance on Condition 1C. Perhaps more significantly, TI subjects took as long to reach criterion on 2A as 1A. In contrast, TE subjects reached criterion on 2A faster than TI subjects. TE subjects did, however, take longer to reach criterion on 2A than 1C, and like TI subjects, took as long on 2A as 1A. For both groups, therefore, the transfer to 2A imposed a cost on performance, a cost that reveals problems with inhibitory control.

Concerning the question of features, we interpret our results as follows. TI subjects appear to have focused more exclusively on colour over either physical/causal support or a combination of features. We defend this interpretation on the basis of the significant cost of reversing colours in 2A. TE subjects, in contrast, either used a pure physical/causal strategy, or a combination of features. Clearly, based on the decrement in performance in 2A, some subjects used colour as a discriminating feature. Had they ignored colour, there would have been no significant change in performance between 1C and 2A; at least two subjects (Fig. 4b) appear to have focused primarily on physical/causal properties of the task, with little to no contribution of colour. Overall, then, TI subjects focused on colour, while TE subjects used both colour and physical/causal support. These results reinforce the parallel findings from the animal-learning literature (Mackintosh 1977).

Second, given the features attended to in the initial discrimination, how much difficulty do tamarins have in learning a new discrimination when the association between discriminative feature and reinforcement is reversed? TI subjects incurred the most significant cost during reversal learning. In the transition from 1C to 2A, TI subjects' performance dropped to the level of Condition 1A, the initial task. Furthermore, when transferred to 2B, a condition involving the original colour–reward associations of Phase 1, their performance dropped below that shown on 1B or 1C. This shows that TI subjects maintained their focus on colour when tested on 2A, and thus, were forced to inhibit the most recently reinforced colour when tested on 2B. In contrast to TI subjects, TE subjects had less difficulty with Phase 2. None the less, they required several sessions to reach criterion on 2A, the first reversal, and required a comparable number of sessions on the second reversal (2B) as well as the final condition, which eliminated the colour association. This shows that TE subjects also relied, to some extent, on colour to solve the initial discrimination. Overall, then, reversal learning was difficult for both groups, highlighting once again the point that tamarins have difficulty with problems of inhibitory control (Rumbaugh 1997; Hauser 1999; Hauser et al. 1999; Hood et al. 1999; Santos et al. 1999).

Third, does domain-specific expertise on a problem change the process of reversal learning, and consequently, of inhibitory control? As emphasized above, TE subjects showed consistent differences in performance throughout the experiment, most notably on conditions 1A and 2A. Although it is possible that the TE subjects were, by chance, 'smarter' than the TI subjects, we suggest instead that the differences between groups were due to domain-specific experience. Specifically, because we ran TE subjects on a series of experiments involving tool use, they appear to have acquired some domain-specific experience with respect to the featurally relevant properties of the task. When tamarins use tools, they base their selection of objects on functionally relevant (i.e. shape, material, orientation) as opposed to irrelevant features (i.e. colour, texture). Thus, if a blue cane represents an effective tool, then so does a purple, yellow, pink or red cane. However, if the object's shape or material is changed in such a way that it can no longer effectively retrieve the reward, tamarins reject such objects in favour of ones that can (Hauser 1997; Hauser et al. 1999; unpublished data). Although TE and TI subjects reached criterion on Conditions 1B and 1C at approximately the same time, TI subjects took approximately twice as long on Condition 2A, the first reversal session. We suggest that this difference was due to the fact that TE subjects solved Phase 1 by attending to both physical/causal support and colour, thus reducing the extent to which inhibitory control was necessary. Returning to the continuity–noncontinuity distinction, TE subjects built a weaker association between colour and reward than TI subjects because colour was only one of the features used in discrimination. For TI subjects, colour was the only predictor of reinforcement, and thus, was more difficult to inhibit during the reversal conditions; this pattern fits with the animal-learning literature on the acquired distinctiveness of cues that was pioneered by Lawrence (1950).

The distinction between domain-specific and domain-general performance is certainly not novel (Carey & Spelke 1994; Cosmides & Tooby 1994; Pinker 1997; Hauser 2000; Shettleworth 1998; Santos et al., in press). What we believe is novel is the relationship between domain-specific experience and problems of inhibitory control, especially with respect to both the continuity–noncontinuity distinction as well reversal learning. As discussed above, most studies of continuity–noncontinuity and reversal learning have used relatively abstract, nonbiological stimuli such as geometric shapes. Such stimuli do not afford clear tests of domain-specific experience. What we have added to this rich literature is the idea that prior experience in particular domains may affect the degree of inhibitory control, and the extent to which particular features are more or less salient with respect to discrimination learning (Garcia & Koelling 1966; Bolles 1984; Revusky 1984). Although we have focused here on the domain of tools, or artefacts more generally, other domains can and should be tested. Thus, although colour appears to play little to no role in assessing the functionality of a tool, colour rather than shape is important for the domain of food (Santos et al. 2001), while spatial geometry is important for certain kinds of orientation (Cheng 1986; Hermer & Spelke 1994; Gouteux et al. 2001). Future work must explore how these different domains, and the learning mechanisms with which they are associated, guide problem solving, including discrimination learning and the role of inhibitory control.

The difference in performance between TE and TI subjects raises one final point that we consider relevant to all studies that use the same subjects in a wide variety of experiments. Although most studies cite the kinds of experiments that their subjects have participated in previously, few explore directly how previous experience on one class of experiments can affect, positively or negatively, subsequent performance. Our own studies of cottontop tamarins are certainly vulnerable to this criticism, and the present work shows why. To clarify, consider the possible results of a slightly different design. Instead of dividing the colony into tool-experienced or inexperienced subjects, we simply divide the colony at random into two groups, half tested on Blue/R+ and half on Red/R+. Under these conditions, if our random assignment of subjects resulted in a mix of tool-experienced and inexperienced tamarins within each group, we would undoubtedly have found little difference in performance between groups. In contrast, if our random assignment placed all the tool-experienced subjects in one group and the tool-inexperienced in the other we would have found, as reported here, significant differences between groups. Having kept track of our subjects' experiences, we may have uncovered the source of such group differences. In conclusion, we consider our results as a warning sign, one that should be considered whenever subjects are tested in multiple experimental tasks. There are potential costs and benefits, as demonstrated by recent studies of so-to-speak 'enculturated' animals, individuals given the experience of a human environment (see Discussion in Premack 1986; Whiten & Custance 1996; Tomasello & Call 1997; Tomasello 1999).

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