



Executive control and task-switching in monkeys

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Abstract

Executive control involves concentrating on one task without losing the ability to switch to a second task at will. We studied this ability in monkeys (*Macaca mulatta*) performing arbitrary stimulus–response mappings in a task-switching paradigm. We found relatively low switch costs but high task interference costs. This is the reverse of the typical human pattern of relatively large switch costs and small interference costs. This difference in the behavior of the two species may reflect anatomical differences in the sizes of the prefrontal and parietal cortices. These results indicate that monkeys are an excellent model for some but not all aspects of human task-switching.

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1. Introduction

Human behavior is not simply stimulus driven, but is also modulated by internal states. Internal control over behavior—usually referred to as executive control (Vandierendonck, 2000)—enables us to respond to stimuli in a task- and goal-dependent way. An important aspect of executive control is the ability to direct attention, or cognitive focus, to relevant stimuli and to maintain attention once it has been directed. An example of this from daily life is that while driving a car we selectively attend and respond to certain traffic-relevant stimuli, like speed limit signs. However, once we get out of the car we rapidly switch our attention to stimuli that were irrelevant during driving, for example, subway entrances.

Executive control requires at least two dimensions of cognitive focus (Luria, 1962). On the one hand there is the flexibility with which we can switch focus from one set of task-relevant stimuli to another, and on the other hand there is the strength with which we can maintain focus and screen out distractors, even when those distractors are relevant in another task. Task-switching paradigms provide a psychophysical method by which to assess these different aspects of cognitive focus (Allport, Styles, & Hsieh, 1994; Jersild, 1927; Meiran, 1996; Rogers & Monsell, 1995;

Spector & Biederman, 1976). Recently, detailed process-oriented models of human executive control have been proposed and quantitatively tested (Gilbert & Shallice, 2002; Kieras, Meyer, Ballas, & Lauber, 2000; Meiran, 2000; Norman & Shallice, 1986). In the present study, we investigate executive control in monkeys using a task-switching paradigm. Our aims are to characterize certain aspects of executive control in animals and to test whether animals provide an appropriate model for human executive control.

In task-switching paradigms, subjects rapidly perform sequences of two interleaved tasks. In our cued task-switching paradigm, the two tasks were randomly interleaved. At the beginning of each trial, subjects are informed about the upcoming task with a task cue (Fig. 1a). After a delay (preparation time), a target stimulus is presented. The task cue instructs which feature of the target should be attended, and how to respond to that feature (Fig. 1b). Thus the task cannot be solved by attending to the target alone. For example, if one task requires a color discrimination and another task a luminance discrimination, one needs to know whether to attend to the color or to the luminance in order to correctly respond to a target containing both color and luminance information.

Studies employing task-switching paradigms have shown limitations of human executive control. Human subjects have difficulty redirecting their attention to a new task (Allport et al., 1994; Meiran, 1996; Rogers & Monsell, 1995; Spector & Biederman, 1976). This has been quantified using *switch costs*, which are operationally defined as the difference between performance in *repetition trials*, in which the

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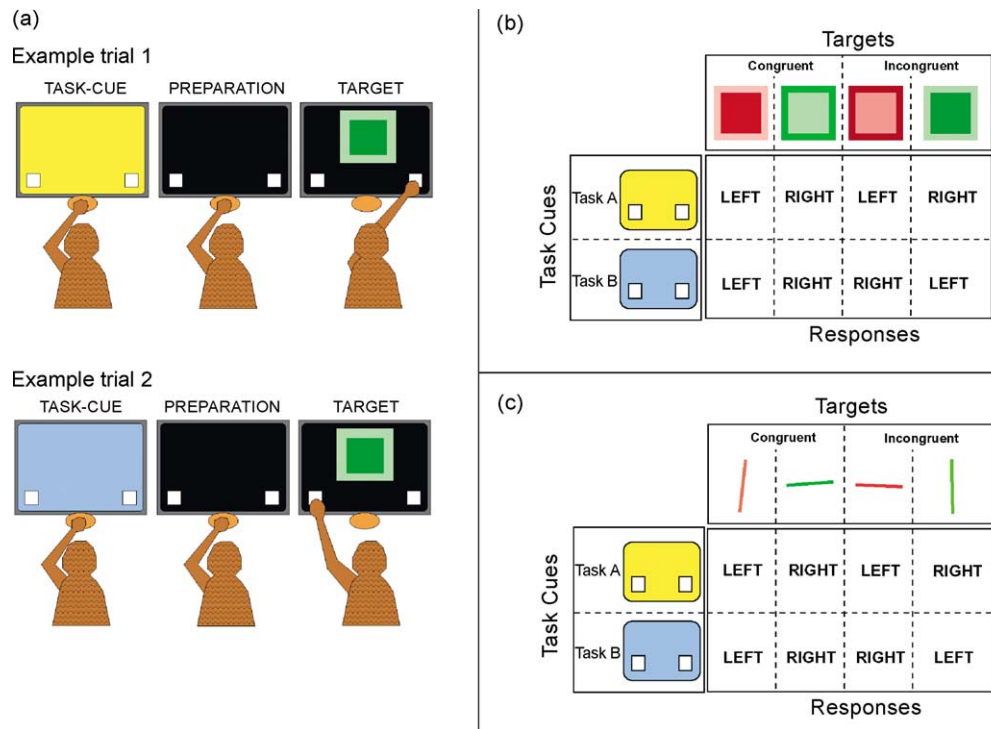


Fig. 1. Task-switching paradigm. (a) Sequence of events in the task-switching paradigm in two example trials. The task cue (yellow or blue background) instructed what feature of the target to attend to; see Section 2. (b) Stimulus–response mappings for cue–target combinations for human subjects and monkey 1. In Task A, red stimuli required a left response and green stimuli a right response. The targets in the top row display some examples of the range of red and green colors. In Task B, stimuli with a brighter outside than inside required a left response, and stimuli with a darker outside than inside required a right response. *Congruent* stimuli (columns 1 and 2) were mapped to the same response button in both tasks; *incongruent* stimuli (columns 3 and 4) were mapped to opposite response buttons in the two tasks. (c) Stimulus–response mappings for monkey 2. We used color and orientation dimensions instead of color and luminance contrast in order to establish the generality of the effects we observed. Task A was the same as for the other subjects. In Task B, vertically oriented stimuli required a left response, and horizontally oriented stimuli required a right response.

task of the previous trial is repeated, and in *switch trials*, in which the task is changed. Since the first report in 1927 Jersild (1927), many studies have confirmed that human performance is slower and less accurate in switch compared to repetition trials. Switch costs decrease with increased preparation time. But even with preparation times exceeding 1 s, subjects still show residual switch costs (Allport et al., 1994; Meiran, 1996; Rogers & Monsell, 1995).

A second limitation of human executive control is captured by *interference costs*, which measure the distraction produced by task-irrelevant stimulus properties. Interference costs are computed as the difference between performance in two types of trials. *Incongruent* trials contain distracting features that, if erroneously attended to, would result in a different and therefore incorrect response. In *congruent* trials, both task-relevant and task-irrelevant features lead to the same (correct) response. In short, incongruent stimuli lead to different responses in the two different tasks, while congruent stimuli lead to identical responses. Many studies have shown that human performance is slower and less accurate on incongruent trials (Allport et al., 1994; Meiran, 1996; Rogers & Monsell, 1995). Interference costs also occur outside of explicit task-switching paradigms. For

example, in the Stroop task (Stroop, 1935) humans have difficulty verbalizing the color of a word, printed in colored ink, when the printed word itself names a different color (e.g. the word ‘red’ printed in green ink). The interference in the Stroop task depends on previously learned associations between printed words and their meaning, while congruency costs in task-switching paradigms are more often instruction based. However, the principle of interference, in which a stimulus is associated with different responses in different task contexts, is common to both paradigms.

2. Methods

2.1. Subjects

Two young adult male Rhesus monkeys (*Macaca mulatta*; both 5 years of age with a weight of 6 kg) and seven healthy adult humans (21–41 years) took part in this study. Use of animals complied with all relevant laws and was approved by the Washington University School of Medicine IACUC Committee.

2.2. Apparatus and stimuli

Stimulus presentation, trial selection, and data collection were controlled by computers running custom software. During data collection, subjects (human or animal) were seated in a sound-attenuating dark room.

Stimuli were projected onto a touch sensitive rectangular screen (30 cm × 20 cm) positioned 25 cm in front of the subjects. A touch sensitive (capacitive) button (*home key*, Efactor Inc.) was positioned 2 cm below the screen. The subjects could freely move their arms and easily touch the screen.

Response buttons were white squares (4.6° of visual angle on a side) at the left and right bottom of the screen. The distance between the two squares was 15.5 cm (33.3°). Task cues were presented by setting the screen color to yellow or blue, or by displaying an upward or downward triangle at screen center. Similar results were obtained using either set of task cues. Targets for humans 1 through 4 and monkey 1 were squares (13.6°) with a luminance contrast between border and inside presented at screen center (Fig. 1a and b). The border and inside each comprised half of the total surface of the stimulus. Target color was randomly chosen from a large number of different shades of red and green (e.g. pink, orange, cyan). The different combinations of color and luminance contrasts yielded 104 different target stimuli. A large range of color and luminance was chosen to encourage the use of general rules rather than 'lookup tables' for solving the tasks. Targets for humans 5 through 7 and monkey 2 were colored lines (6.9 × 0.7°; Fig. 1c). Line color varied as for the other subjects. Lines were oriented within 10° of either the horizontal or the vertical axis.

Eleven novel target stimuli were created using various combinations of a new line orientation (20 or 45° from either the horizontal or vertical axis), a new color (blue), and a new line thickness (1.1°).

2.3. Procedure

Two tasks were randomly interleaved. At the beginning of each trial subjects were informed by a yellow or blue screen which of the two tasks was to be performed. In Task A, the subjects had to judge whether a colored square was red or green, and in Task B whether the square had a brighter inside than outside (Fig. 1b). Subjects pressed a left or right response button to indicate their judgment. In order to ensure that the effects we observed were not specific to the particular tasks we had chosen, the second animal (and half the human subjects) used slightly different stimuli and was trained on a slightly different Task B than the first subject (and the other half of the human subjects) (Fig. 1c; see Section 2).

Each trial started when the subject put its dominant hand on the home key (Fig. 1a). The response buttons appeared immediately and remained on until the end of the trial. After 10 ms, the task cue appeared. After a preparation interval of 500–600 ms, the target stimulus appeared and remained on

screen until the subject moved its hand from the home key. The subject then had 2000 ms to touch within ~6 cm of the left or right response button. We used this generous window in order to encourage a rapid response rather than a precise touch. Reaction time (RT) was measured as the interval between target onset and home key release. Similar results were obtained using the interval between target onset and the acquisition of the response button. Monkeys were rewarded for correct responses with a drop of water (0.05–0.33 ml). Incorrect trials in both species were followed by an error display and a 1 s wait period.

For the monkeys and for three of the seven humans, the task cue disappeared 200 ms into the task preparation interval. This was intended to encourage the subjects to actively process the task cue prior to receiving the target stimulus. For the first four humans tested, the task cue remained on screen throughout the task preparation interval, making the task slightly easier. In these same four humans, the inter-trial interval was shorter than that used with the monkeys and with the final three humans (250 ms versus 345 ms). The shorter inter-trial interval compensated for the fact that monkeys responded to the target stimulus more quickly than humans (see Section 3). The second set of humans served as a control for the differences in timing between the animals and the first set of humans. The results were identical, and we mainly report data from the first set (H1–H4).

3. Results

We first asked whether animals could perform a switching task at a level comparable to human performance. We analyzed reaction times using analysis of variance with the factors switch and interference. For this data analysis we excluded all error trials and trials that immediately followed an error trial. We analyzed percentage of errors (PE) with χ^2 -tests (Fig. 2a). When computed across all trials, performance was similar for the two species. Monkeys were generally faster than humans (mean RT 325 ms versus 440 ms), although RT in the two fastest humans was comparable to that of the slower monkey. On an average, humans were slightly more accurate than monkeys (mean PE = 3.9% versus 5.8%). However, the range of performance for the monkeys overlapped that of the humans. While the two most accurate subjects were both human (H2 and H4, PE = 2.3 and 3.1%), the other two human subjects performed at levels comparable to the two monkey subjects (M1 and H3: PE = 4.7% versus 4.0%; M2 and H1: 6.9% versus 6.3%; differences not significant at $P < 0.05$).

Despite their similarity in overall performance, humans and monkeys show a striking difference in their ability to switch from one task to another. Human reaction times were significantly slowed on the trial immediately following a task switch (Fig. 2b). Switch costs (see Section 1) were large and highly significant for each of the four human subjects ($P < 0.01$). Costs ranged from 21 to 49 ms and had a mean value

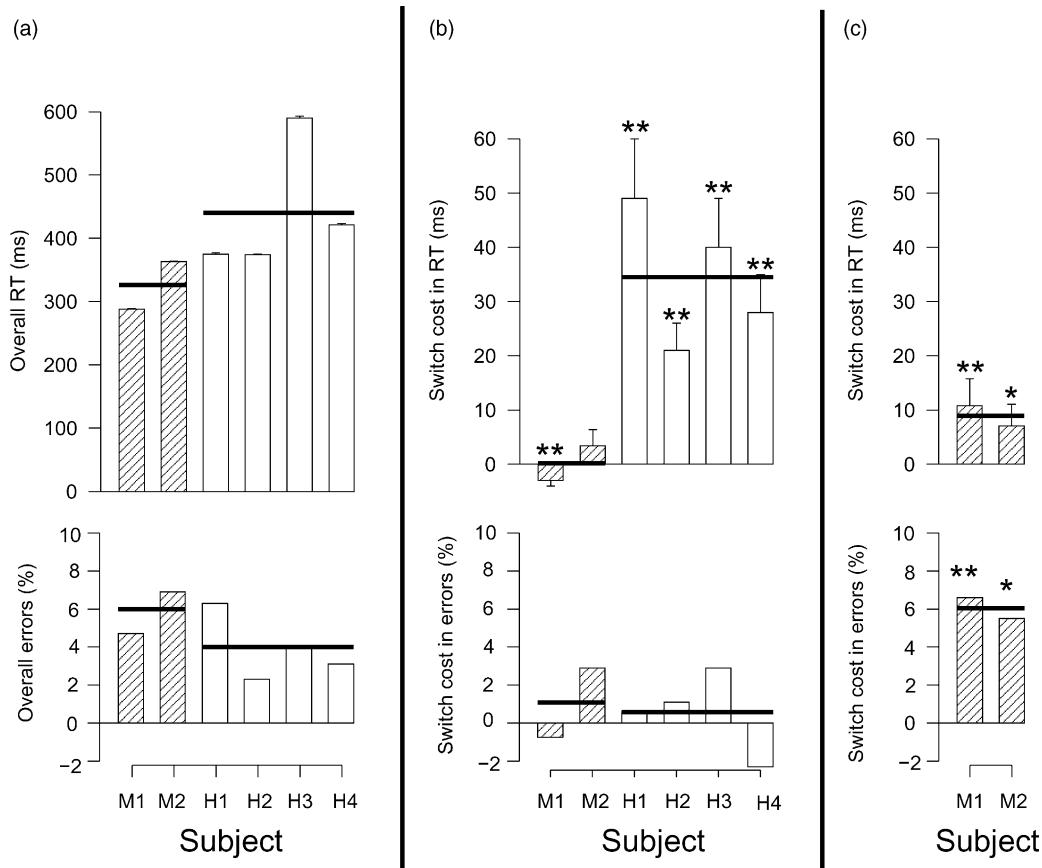


Fig. 2. Humans show switch costs but monkeys do not. (a) Overall performance by monkeys (M1 and M2; shaded) and human subjects (H1–H4; not shaded). Monkeys were faster (above, reaction time (RT)) but had similar accuracy (below, percentage of errors (PE)). Horizontal lines show species means. Error bars show ± 1 S.E.M. for RT. (b) Switch costs in RT (mean RT on switch trials minus mean RT on repetition trials, ± 1 S.E.M.) and PE (PE on switch trials minus PE on repetition trials) in monkeys and humans. Only humans showed significant switch costs in RT ((* $P < 0.05$, (** $P < 0.01$)). Neither humans nor monkeys showed significant costs in PE. This indicates that monkeys, unlike humans, are able to switch their cognitive focus to a new task without cost. Human data are taken from the final day of testing (see Fig. 3). (c) Switch costs appeared in monkeys when short intertrial intervals were used (170 ms).

of 35 ms. Results were similar in the second set of subjects (costs ranged from 20 to 49 ms with a mean switch cost of 31 ms in RT and 1% in PE). In contrast, neither monkey showed a significant switch cost, in either RT (mean cost = 0.2 ms) or PE (mean cost = 1%).² There are many studies in which animals have been trained on multiple tasks, and in one study two monkeys performed a task very similar to ours (Wallis, Andersen & Miller, 2001). However, ours is the first study to report on the presence or absence of switch costs in monkeys.

An important difference between most experiments in humans and monkeys is the amount of practice that the subjects receive. In most human psychophysical experiments, subjects get a verbal instruction and a few training trials before data is collected. In contrast, monkeys are usually trained

² Subject M1 had a small but significant negative switch cost (i.e. a switch benefit of 3 ms) in the original experiments. On subsequent testing, we were unable to reproduce this effect, and therefore believe it to be a false positive.

extensively before data is collected. Our animals had about 100,000 practice trials before data was collected. This level of practice is not unusual among trained humans. Professional athletes or musicians may practice a particular task hundreds of thousands or even millions of times, for example. It is possible that extensive practice leads to a diminution or abolition of switch costs. In order to test this idea, we trained our first four human subjects in six sessions of 504 trials each. Sessions were separated by at least 1 day. As expected, we found that overall performance improved with practice, that is, reaction time and error percentage decreased (Fig. 3a). We calculated a linear regression on the mean switch costs (Fig. 3b) and found significant positive slopes, indicating that switch costs increased with training (5.6 ms per session; $F(1, 22) = 8.83$, $P < 0.01$). We also observed a drop in switch PE across sessions (-2.4% per session; $F(1, 22) = 6.56$, $P < 0.05$). The opposite evolution of switch-costs in reaction time and accuracy with ongoing practice of the task suggests that humans changed

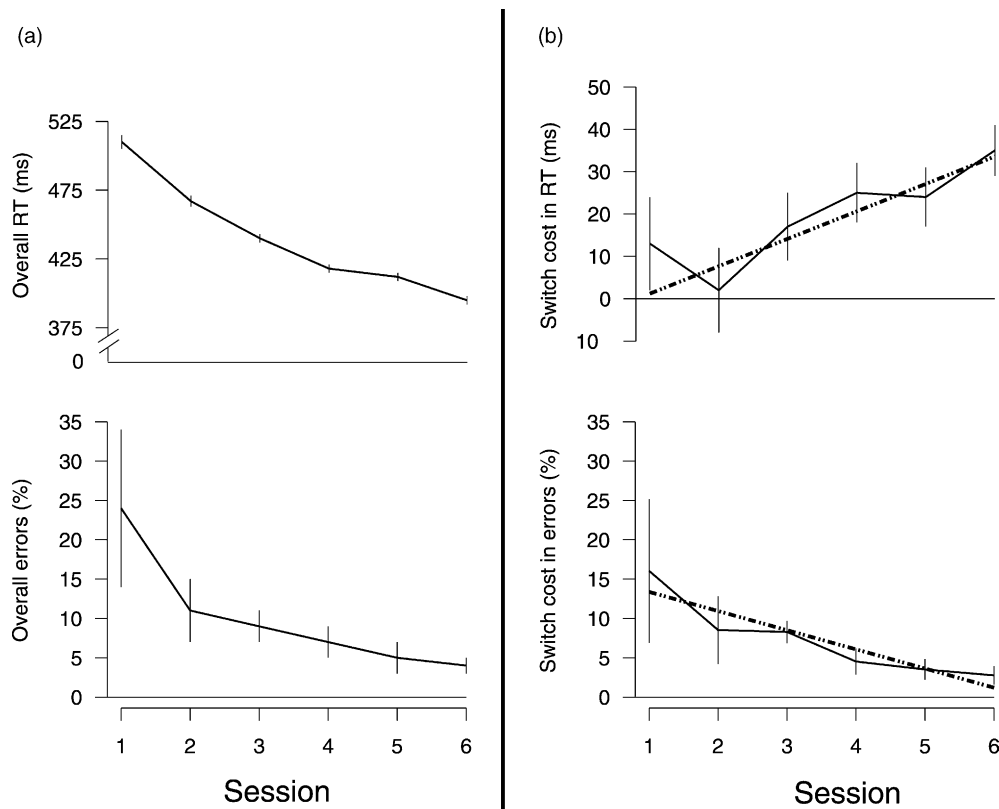


Fig. 3. Practice effects do not explain the lack of switch costs in monkeys. (a) Overall RT (± 1 S.E.M.) and error rates as a function of training sessions, averaged over four human subjects. Performance improved steadily as a result of practice. (b) Switch costs in RT and PE as a function of training session. Broken line displays least squares regression. Switch costs in RT did not go away during training, but instead increased.

their speed–accuracy trade-offs. Despite the development of a speed–accuracy trade-off during training, switch costs did not disappear, but instead remained robust right up until the sixth session. Thus, in agreement with previous studies (Kramer, Hahn & Gopher, 1999; Rogers & Monsell, 1995), training did not abolish human switch costs. Similar results were obtained in human subjects H5–H7.

Switch costs may arise in at least two ways. First, there may be task inertia, that is, a lingering representation of the previous task set which inhibits the installation of a new task set (Allport et al., 1994). Second, the installation of a new task set, that is, the reconfiguration of neural circuits to perform a new task, may remain incomplete until a stimulus for that task is actually received. Both mechanisms are thought to contribute to human switch costs (Allport et al., 1994; Meiran 1996). Evidence for a role of task inertia is provided by the fact that human switch costs decrease with increasing preparation time, as if the effect of the previous task wears off over time (Meiran, 1996). However, even with long preparation or intertrial intervals (e.g. 1.6s), human switch costs are not completely abolished (Meiran, 1996). The persistence of residual switch costs even after the representation of the previous task has had ample time to wear away suggests that the installation of the new task remains incomplete until a stim-

ulus actually arrives (Meiran, 1996; Rogers & Monsell, 1995).

The absence of residual switch costs in monkeys (Fig. 2b) suggests that in monkeys, unlike humans, neural circuits can be completely reconfigured to perform a new task prior to the arrival of the first stimulus. Thus, the second of the two mechanisms just described for generating switch costs in humans does not seem to operate in highly trained monkeys. In order to test whether the first mechanism for switch costs operates in monkeys, that is, whether lingering representations of previous tasks might conflict with the installation of a new task, we compared blocks of trials using short (170 ms) versus long (345 ms) intertrial intervals (ITI). We found significant switch costs in both monkeys in the short ITI blocks (11 and 7 ms in RT; 6.6 and 5.5% in PE, all measures different from zero at $P < 0.05$; Fig. 2c). Thus, in the monkey, small switch costs may arise as a result of a conflict between a lingering representation of a previous task and the installation of a new task. In contrast to the case in humans, however, this lingering representation decays very quickly, so that at an ITI of 345 ms the effect is no longer present in the monkey.

Switch task paradigms require not only the ability to switch from one task to another, but also the ability to focus on the task currently at hand. Part of focusing on the task

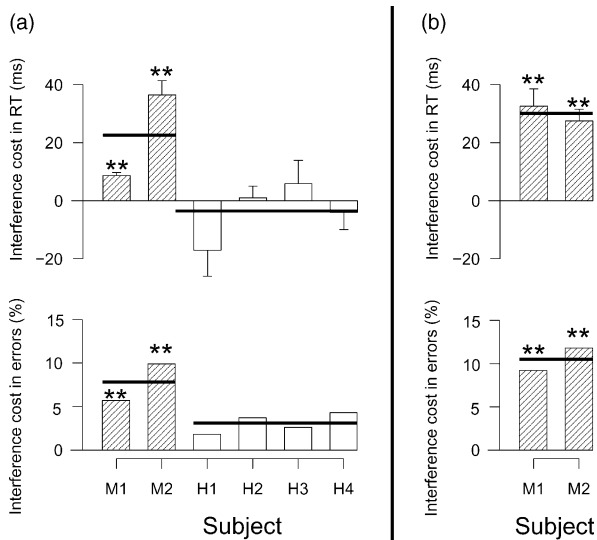


Fig. 4. Monkeys show interference costs but humans do not. (a) Interference costs in RT (mean RT in incongruent trials minus mean RT in congruent trials) and PE (PE in incongruent trials minus PE congruent trials) are plotted for each subject. Effects were significant in both RT and PE for both monkeys, but for none of the humans. This indicates that monkeys but not humans are distracted by stimulus features that are irrelevant to the current task. Format as in Fig. 2b. One human subject (H1) appears to show an interference benefit, but this effect was not statistically significant. (b) With short intertrial intervals, interference costs increased in both RT and PE in monkeys.

at hand is the ability to attend only to those stimulus features which are relevant, and to ignore those which are irrelevant. Interference costs (see Section 1) measure the extent to which a subject fails in this ability.

As illustrated in Fig. 4a, both animals showed clear interference costs in RT (9 and 36 ms, both significant at $P < 0.01$) as well as in PE (5.7 and 9.9%, both significant at $P < 0.01$). In contrast, human subjects did not show a significant effect in either RT (mean value -4 ms) or PE (mean value 3%). Consistent results were found with a shortened ITI in monkeys: interference costs in both RT (33 and 28 ms) and PE (9.2 and 11.8%) were both highly significant (Fig. 4b).

A reason that animals may fail to show switch costs comparable to those of humans relates to strategy. Although we have used a wide range of different target stimuli to promote the use of abstract task rules, it is conceivable that monkeys have learned each cue–target–response combination, and employ a ‘lookup table’ strategy to solve the task. If animals learn specific cue–target–response combinations rather than general rules, then they should fail to perform above chance on novel stimuli. To distinguish between these two strategies, we introduced eleven novel stimuli to monkey M2 interspersed with the practiced target stimuli. Each novel stimulus was presented only once. The animal performed correctly in 10 out of 11 novel trials. This is significantly greater than chance ($\chi^2(1) = 7.4$, $P < 0.01$), indicating that the animal had learned to apply general rules.

4. Discussion

We studied executive control in two monkeys with a task-switching paradigm. To determine whether our task-switching paradigm would result in switch costs in humans, we studied seven human subjects. We found that overall performance is similar in the two species, although monkeys were somewhat faster than humans (Fig. 2a). We do not take the faster reaction times in monkeys compared to humans as evidence of superior behavioral performance. For example, physical differences in the conduction pathways of the smaller brain (Ringo & Doty, 1994) or mechanical factors in the musculature could partially explain the differences in performance. On the contrary, we feel that having monkey reaction times so similar to those of the humans (e.g. M2 differs from H1 and H2 by less than 15 ms) legitimizes the interspecies comparison of second order measures of behavioral performance such as switch and interference costs.

Monkeys show no difficulty in switching their attention from one task to another (little or no residual switch costs; Fig. 2b). However, their ability to focus on the task at hand is comparatively poor: their performance is significantly affected by irrelevant stimulus features (high interference costs; Fig. 4). The opposite is true for humans, who have difficulty switching but little difficulty maintaining attention on the appropriate stimulus features (Figs. 2b and 4).

The difference between human and monkey performance could represent a true species difference. However, an alternative explanation is that the 3000 practice trials performed by our human subjects did not adequately control for 100,000 practice trials performed by our monkeys (Fig. 3). In our training data, switch costs remained robust right up until the sixth session. More extensive practice in humans might drive their switch costs to zero as well. However, a small number of studies report a decrease in switch costs with training (Kramer et al., 1999; Rogers & Monsell, 1995), but none have shown a complete loss. Yet, if extensive practice results in switch costs being driven to zero, one would expect that interference costs would similarly be driven to zero. Instead, interference costs remain high in monkeys even after extensive training (Fig. 4a).

Another potential explanation for our results is that monkeys, relative to humans, are biased towards speed over accuracy. This speed–accuracy trade-off is suggested by the fact that, in overall performance, monkeys were faster but less accurate than humans (Fig. 2a). From this one might predict that monkeys would respond to switch trials with a large increase in error rate and only a small increase in reaction time. While this explanation is consistent with the data of monkey 2, it cannot explain the data of monkey 1, who showed no switch costs whatsoever, either in reaction time or in error rate (Fig. 2b).

We also considered the possibility that monkeys memorized all 208 separate cue–target–response combinations,

and then used a ‘lookup table’ strategy. Two pieces of evidence refute this idea. First of all, we found small switch costs when intertrial intervals were very short, suggesting that monkeys treat the two tasks differently. Second, an animal successfully responded to completely novel stimuli, which the animal would not be able to do if it used a cue–target–response ‘lookup table’ strategy.

Finally, as in many comparative studies, we cannot rule out the possibility that some inadvertent difference in procedure may have contributed to our results. For example, animals but not humans were rewarded with drops of water for each correct response. As another example, only the humans were provided with a verbal description of the task (although one human was intentionally left to work out the task in the same way that the animals did, and her performance was similar to those of the other humans).

In comparing humans with monkeys, the presence of persistent switch costs and lower interference costs could be two manifestations of a single process. Humans apparently can ‘lock in’ to a particular task, thereby minimizing interference costs but paying the price of having to take time to ‘unlock’ the mapping when the task switches—hence the appearance of persistent switch costs. Both humans and monkeys show non-persistent switch costs, that is, costs that appear only with short preparation times. Non-persistent switch costs may therefore reflect an independent process by which both humans and monkeys instantiate a particular stimulus–response mapping. This independent process supports the ability to switch between tasks rapidly, but neither protects against task interference nor incurs persistent switch costs.

Thus we suggest that monkeys share some processes related to task-switching with humans, but monkeys lack at least one mechanism, which in the human leads to prominent persistent switch costs and low interference costs. Task representation and switching is traditionally thought to be mediated by the prefrontal cortex (PFC). For instance, brain imaging studies of switch costs in healthy humans show that switch costs are related to enhanced brain activity in prefrontal areas (Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Gurd et al., 2002; Pollmann, Dove, von Cramon, & Wiggins, 2000; Sohn, Ursu, Anderson, Stenger, & Carter, 2000). Single neuron studies in monkeys performing paradigms similar to task-switching did not address the question of switch costs, but did find task specific signals in the PFC (Hoshi, Shima, & Tanji, 1998, 2000; Wallis et al., 2001; White & Wise, 1999). Other animal studies have reported neural correlates of various other executive functions in the PFC, including the storage, use and acquisition of task rules (Bussey, Wise, & Murray, 2001; Dias, Robbins, & Roberts, 1996). However, imaging data in humans as well as preliminary work in monkeys suggests a role for the parietal cortex in task representation and even in task-switching (Dove et al., 2000; Gurd et al., 2002; Pollmann et al., 2000; Sohn et al., 2000; Stoet & Snyder, 2002). Both the parietal cortex and the PFC are greatly

expanded in the human compared to the monkey (Semendeferi, Lu, Schenker, & Damasio, 2002; Simon, Mangin, Cohen, Bihan, & Dehaene, 2002; Van Essen et al., 2001). The process or processes which allow humans to eliminate interference costs at the price of paying persistent switch costs are likely to reside in one or both of these expanded cortical regions.

In conclusion, the issue of whether the monkey is a good model for human task-switching is complex. They are a poor model for looking at persistent switch costs, a second order but very consistent feature of human task-switching. Persistent switch-costs are very interesting, and their absence in the monkey makes the monkey a less than ideal model for human task-switching. However, there are many aspects of task-switching that humans and monkeys share, and for these processes monkeys make excellent models. In particular, the macaque monkey is a good model for the ability to switch between tasks (since monkeys, like humans, can learn to switch between tasks quite well); a good model for the ability to prepare tasks in advance (Stoet & Snyder, 2001, *in press*); a good model for task interference; a good model for non-persistent switch costs; and a good model for looking at task representations.

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