ORIGINAL ARTICLE

Gijsbert Stoet · Lawrence H. Snyder

# Task preparation in macaque monkeys (*Macaca mulatta*)

**Abstract** We investigated whether macaque monkeys possess the ability to prepare abstract tasks in advance. We trained two monkeys to use different stimulus-response (S-R) mappings. On each trial, monkeys were first informed with a visual cue which of two S-R mapping to use. Following a delay, a visual target was presented to which they would respond with a left or right button-press. We manipulated delay time between cue and target and found that performance was faster and more accurate with longer delays, suggesting that monkeys used the delay time to prepare each task in advance.

**Keywords** Sensory-motor transformation ·
Stimulus-response mapping · Task switching

## Introduction

Humans can respond to a particular stimulus in accordance with any number of different task rules, or stimulus-response (S-R) mappings. For example, subjects can be instructed to raise their right hand if they are presented with an odd number, and to raise their left hand if they are presented with an even number. That same subject can then be instructed to switch to a different S-R mapping, for example, raise the right hand if presented with a number starting with the letter "T", and otherwise raise the left hand. The ability to prepare a particular S-R mapping, even before a target stimulus has been presented, has been studied in humans using task-switching paradigms (Meiran 1996; Rogers and Monsell 1995; Vandierendonck 2000). In a task-switching study, a subject is instructed which S-R mapping to apply at the start of each trial. After a short

delay, a target is presented, and the subject must respond as quickly as possible, in accordance with the previously instructed S-R mapping. A consistent finding is that response time depends on the duration of the delay between the S-R instruction and the stimulus. Humans respond faster and more accurately with longer delays (Meiran 1996; Rogers and Monsell 1995).

An important aspect of the task-switching paradigm is that, during the delay period between the S-R instruction and the target presentation, the target stimulus is not yet known. As a result, the delay period cannot be used to prepare a particular response or to anticipate a particular stimulus. Task-switching paradigms were specifically designed to study the process of abstract task preparation, that is, preparation for a task in the absence of information about the particular stimulus or response. Of particular interest is the neural substrate of task preparation. Psychophysical and brain imaging studies have been performed in humans in order to address this issue (Cherkasova et al. 2002; Dove et al. 2000; Gilbert and Shallice 2002; Kavcic et al. 1999; Konishi 2002; Kramer et al. 1999; Le et al. 1998; Moulden 1998; Pollmann et al. 2000; Sohn et al. 2000; Wylie and Allport 2000). Single neuron recording in an animal model would be desirable, though so far there is no animal model of task-switching, although several studies have come close to such a model (Eskandar and Assad 1999; Wallis et al. 2001), but see (Stoet and Snyder 2003).

Advance task preparation in animals has been investigated at both behavioral and neurophysiological levels using paradigms other than task-switching. In match-to-sample experiments, for example, the appearance of an initial sample stimulus enables an animal to select a matching stimulus at a later stage in the trial. Animals could use a memorization strategy or a preparation strategy to solve such a task. In particular, the sample stimulus itself could be stored (retrospective memory), or identifying features of the anticipated match stimulus could be stored (prospective memory) (Rainer et al. 1999). Current evidence indicates that animals employ both retrospective and prospective strategies. The use of a prospective memory strategy indicates that animals are capable of advance task prepa-

G. Stoet (✉) · L. H. Snyder
Department of Anatomy and Neurobiology,
Washington University School of Medicine,
660 S Euclid Ave., Box 8108, St. Louis, MO 63110, USA
Tel.: +1-314-7474095, Fax: +1-314 -7474370,
e-mail: stoet@pcg.wustl.edu

ration when specific information is available regarding the upcoming target (Rainer et al. 1999). Similarly, in studies of foraging, behavior is facilitated when information regarding the desired target is available (cf., Pietrewicz and Kamil 1979; Reid and Shettleworth 1992).

Thus it is clear that animals are able to prepare tasks in advance when there is concrete knowledge regarding the upcoming target. We were interested in whether advance preparation may occur when only abstract information is available. In humans, this can be illustrated by a verbal task-switching paradigm. We might instruct subjects to prepare to respond with either a synonym or an antonym to the next word they hear. Prior to receiving the imperative stimulus, do humans prepare for either task in a task-specific manner? Since the instructional cue ("synonym" or "antonym") does not constrain what word may subsequently be presented, the conventional notion of a prospective memory strategy does not apply. Subjects may simply remember the instruction (a retrospective memory strategy), they may prepare for a verbal utterance (a prospective strategy, but one which is identical in the two tasks), or they may employ a strategy which results in faster performance on just one of the two tasks (task-specific abstract task preparation).

In a non-verbal two alternative forced-choice task-switching paradigm, a strategy which results in faster performance in just one of the two tasks could be described as preconfiguring circuits involved in selective attention. While it is clear from many studies that selective attention can modulate neuronal response to target stimuli, especially in the posterior parietal cortex, PPC (e.g., Cook and Maunsell 2002), these studies have focused on what happens once an imperative stimulus has been delivered, not on what happens prior to stimulus delivery. Prior to undertaking studies directed at the neural correlates of such advance preparation, it is advisable to first establish whether or not advance preparation occurs in an animal model. For this, the appropriate approach is a behavioral study. We therefore used a task-switching paradigm to test whether monkeys, like humans, would show improved performance when they are given more time to prepare in the time interval after the instructional cue but before the imperative stimulus.

## Experiment 1

Monkeys rapidly performed randomly ordered sequences of two tasks. Each trial started when the subject touched the home key (Fig. 1a). The response buttons then appeared and remained on screen until the end of the trial. Next, the task cue appeared for 160 ms, followed by a blank screen for either 10 ms (short delay) or 230 ms (long delay). Animals therefore had a total of either 170 or 390 ms to prepare the task. Finally the target stimulus was presented and the animal had to reach to either the left or right response button.

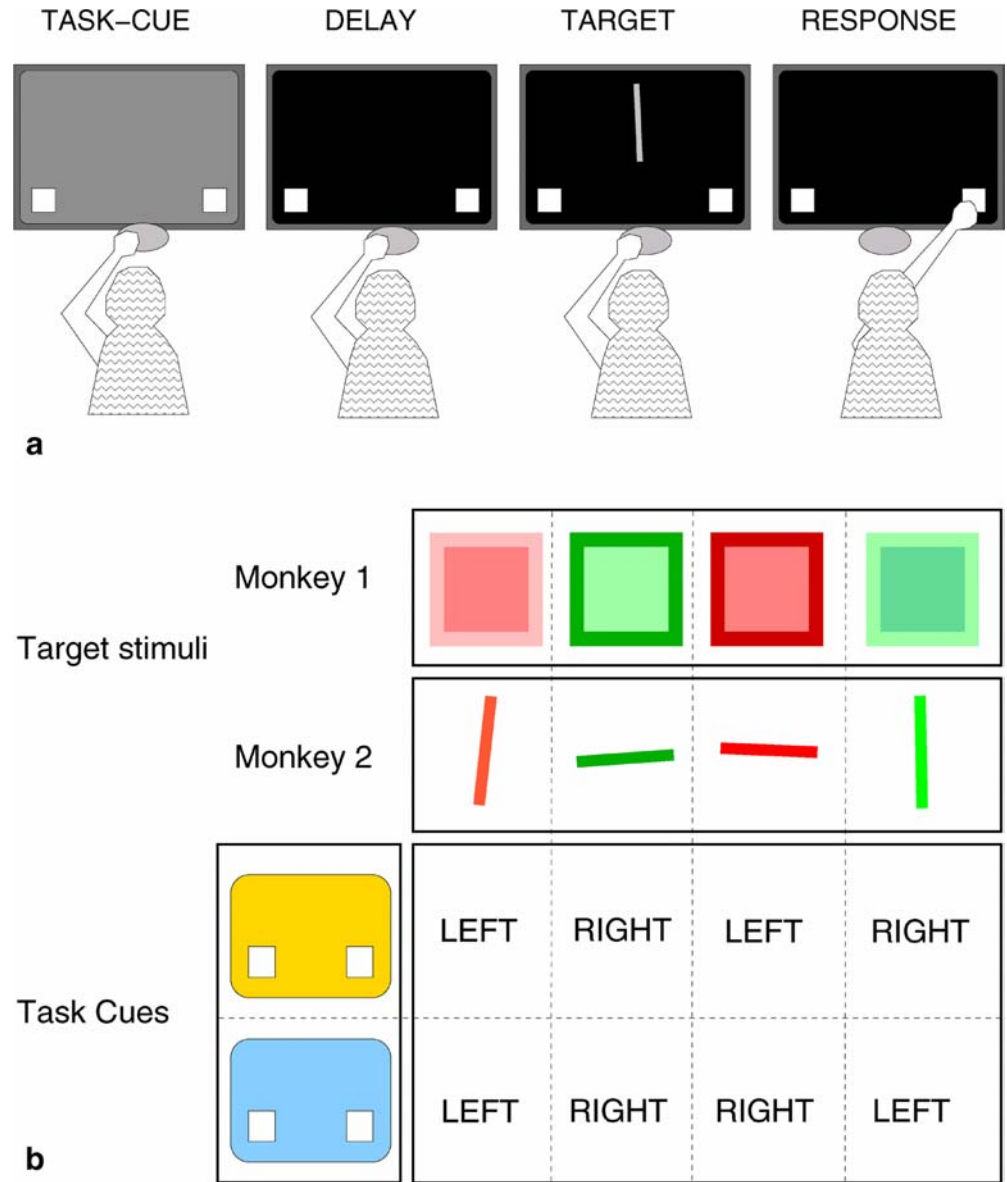In order to ensure the generality of our results, the two monkeys performed different tasks (Fig. 1b). Targets for monkey 1 were colored squares presented near the center of the screen. The border of each target square was the same color but a different luminance from the inside of the square. In task A, the animal was required to discriminate whether the target square was red or green and to respond by pressing the left or right button, respectively. In task B, the animal was required to discriminate whether the luminance of the outside of the target square was brighter or darker than the inside, and to respond by pressing the left or right button, respectively. Monkey 2 responded to colored lines. In task A, the monkey was, like monkey 1, required to make a red versus green discrimination. In task B the monkey had to discriminate whether the line orientation was horizontal or vertical with a left or right button press.

Because identical sets of stimuli were used in tasks A and B, and because some stimuli required different responses in the two tasks, successful performance required that animals utilize the task cue given at the start of each trial. Two different strategies can be applied with regard to the task cue. One strategy is to actively prepare the indicated task during the delay period (Meiran 1996, Rogers and Monsell 1995). We refer to this as the *preparation* strategy. We make no assumptions about the form of this preparation. In this case, it is not the memory of the cue per se that is used for performing the task. An alternative strategy is to merely remember the task cue until the target stimulus appears. In the *memorization* strategy, each cue-target pair is considered as a single stimulus, and that stimulus is then mapped onto a particular response. In the memorization strategy, unlike the preparation strategy, there is no advance task preparation.

To distinguish between a preparation and memory strategy in task switching, we employed a model of information processing inspired by Sternberg's stage analysis (Sternberg 1969, Sternberg 2001) (Fig. 2). Stage models are based on the assumption that information processing can be broken down into serial stages, like sensory encoding, motor preparation, etc. The overall response time is the sum of the time needed for the individual stages. (In fact, strict summation is not required, but the logic of the experiment is easier to follow with this simplification.) Based on this model, we expect that a longer delay will lead to better performance (faster responses and fewer errors) in conjunction with the preparation strategy but not in conjunction with the memorization strategy. Only with the preparation strategy is the delay actually used for processing; in the memory strategy, the cue is simply stored in memory during this interval. This suggests that shortening the delay will degrade performance in the preparation strategy (less time to prepare), while shortening the delay will leave unchanged or even improve performance in the memory strategy (less time to forget).

However, at some point the interval between the cue and target may become so short that additional time is required to process what has essentially become two simultaneous stimuli. We assume that the simple task cues we employ will require identical amounts of time to encode and store (an assumption that we test in a separate control experiment). Therefore, if the memorization strategy is

**Fig. 1a, b** Description of paradigm. **a** Schematic view of the screen, home key, and the monkey from the rear. Each trial starts with the presentation of a task cue (*blue* or *yellow screen*). The cue was followed by a variable delay period, which was then followed by presentation of the target stimulus. The target disappeared as soon as the animal released its hand from the home key. On each trial the monkey touched either the left or right response button. **b** The tasks were different for the two monkeys. Monkey 1 responded either to target color or to target luminance contrast. Monkey 2 responded either to target color or line orientation. The table indicates the required response for each cue and target combination for each monkey



employed, we predict that a shorter delay duration will have identical effects on performance of the two tasks. In contrast, if the preparation strategy is employed, shortening the delay duration is likely to have differential effects on performance, since the advance preparation required for each task will by definition be task-specific, and therefore unlikely to be identical.

Figure 2 illustrates this point. To begin with, we do not assume that either advance preparation or performance time will be identical for the two tasks. We have arbitrarily assigned a longer preparation time to task B, and a longer performance time to task A. On the one hand, in the long delay condition (upper panel), both tasks are fully prepared long before the target appears. Therefore there is no effect of task preparation time on response time. Instead, response time is determined by how long it takes to perform the previously prepared task. On the other hand,

in the short delay condition, task preparation is still incomplete when the target appears (lower panel). As a result, the reaction time measured from target onset is slowed, but since task B takes longer to prepare, task B is slowed more than task A.

In contrast, consider the effect of delay in the memorization strategy (not illustrated). Here the unequal preparation times are replaced by equal memorization times, and as a result, shortening the delay will always have exactly the same effect on task A as on task B. Thus, differential effects of delay duration on task performance are evidence for the preparation strategy, while similar effects are evidence for the memorization strategy.
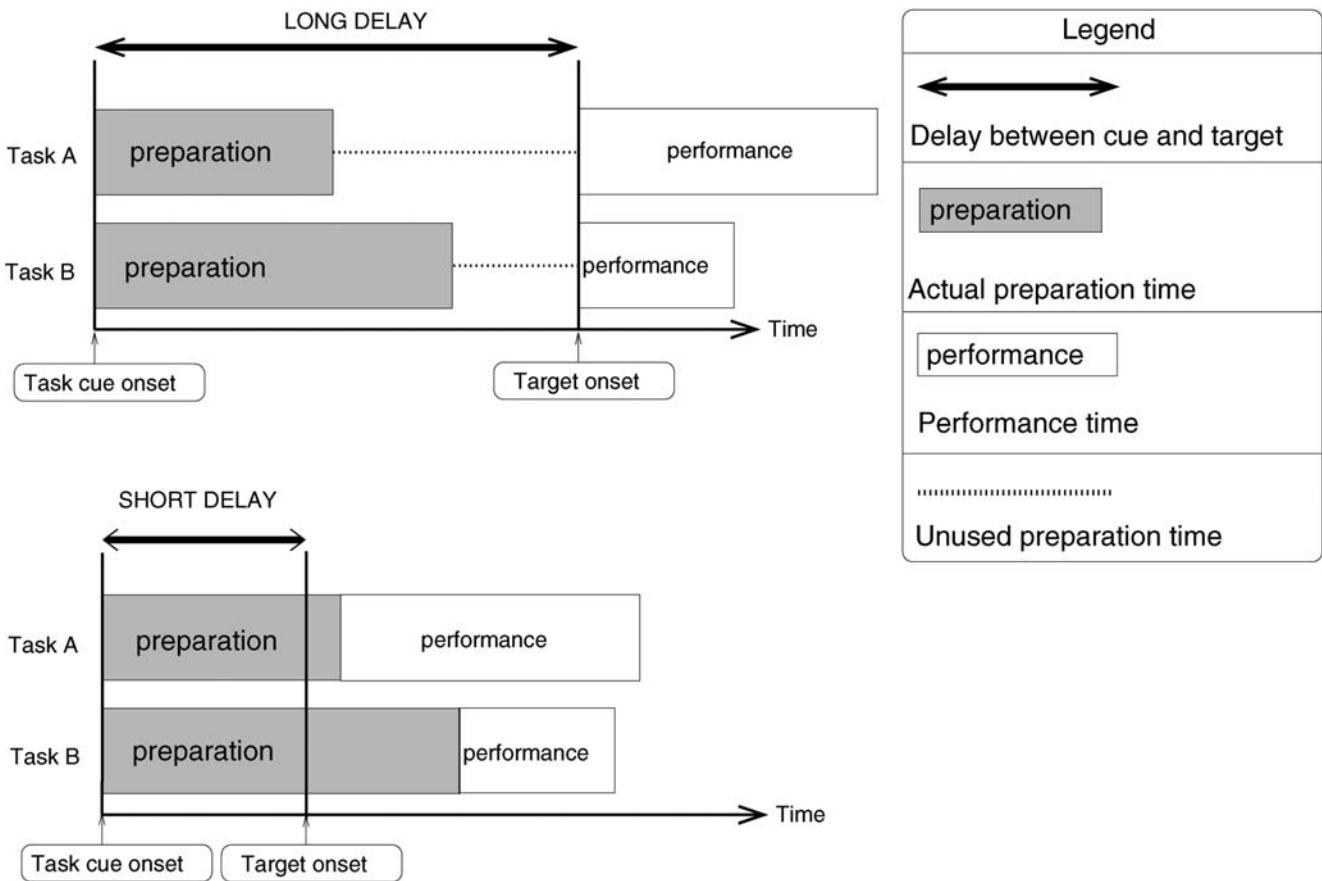
**Fig. 2** Model of information processing during task-switching paradigm. Stages of information processing are task preparation (*preparation*) and task performance (*performance*). It is assumed that these stages are performed sequentially. It is also assumed that cue identification takes the same amount of time in the two tasks, while preparation and performance may differ. (The assumption regarding equal cue processing time is tested in experiment 2; see Figs. 4, 5, 6). The particular stage durations in this figure were chosen arbitrarily to illustrate the principles of the model. With a long enough delay, the time required to complete the task is independent of the time required for task preparation. With a short delay, however, the time required to complete the task will depend on the task preparation time. As a result, an interaction between Task and Delay on reaction time (RT) will indicate the presence of task-specific advance preparation

## Methods

### *Subjects*

The subjects were two 4-year-old male macaque monkeys (*Macaca mulatta*). Monkeys were water deprived and worked for liquid rewards during experimental sessions.

### *Apparatus*

Stimulus presentation, trial selection, and data collection were controlled by computers running custom software. Data collection took place in a sound-attenuating dark room. Monkeys were seated within primate chairs (Crist Instruments, Damascus, Md.), which allowed monkeys to use their forelimbs.

Stimuli were projected onto a touch sensitive rectangular screen (30×20 cm, Magic Touch, Keytec, Richardson, Tex.) positioned 25 cm in front of the monkeys. A touch sensitive (capacitive) button (*home key*, KI2015FRKG, Efector, Exton, Pa.) was positioned 2 cm below the screen. This button functioned as a home key where the left paw rested until a response was required. The animals could freely move their forelimb and easily touch the screen.

### *Stimuli*

Two white squares in the left and bottom right corners of the screen functioned as response buttons and were visible throughout the entire trial.

Targets for monkey 1 were squares (13.6°) presented near the center of the screen (Fig. 1b). Target color was randomly chosen from a large number of different shades of red and green (e.g., pink, orange, cyan). The border of each target square (comprising half the total area) was the same color but a different luminance from the inside of the square. Targets for monkey 2 were lines, measuring 6.9° in length and 0.7° in width (Fig. 1b). Color was varied as for monkey 1. For both monkeys we added random variability to the stimuli. We varied color and luminance for monkey 1, and color and line orientation (±10°) for monkey 2. Each animal had a total of 104 possible targets.

## Procedure

Monkeys were trained using operant conditioning while they were water deprived. The animals were first trained to a criterion level of accuracy of 80% on each of the two tasks separately. After the monkeys had mastered the tasks individually we interleaved single task blocks of trials and introduced the task cues. We gradually shortened the cue display time and lengthened the delay between cue presentation and target stimulus presentation. We also gradually decreased the size of the blocks until the animals were able to perform randomly interleaved trials of both task types. Monkeys 1 and 2 were trained for 21 and 9 months before this study took place, respectively.

Correct responses were rewarded with a drop of water. The total number of trials is indicated by the degrees of freedom in the statistical *F* tests (*n*-1; see Results and discussion). Incorrect responses or key release prior to target appearance resulted in a bright flash and a 1 s time out. We measured performance by reaction time (RT) and percentage of errors (PE). Reaction time began with the appearance of the target stimulus and ended with the release of the home key.

## Results and discussion

Reaction time and percentage of error were computed as functions of the experimental factors Task and Delay (Fig. 3). In the RT analysis we excluded data from error trials and first trials following an error. We analyzed RT data with a two way analysis of variance (ANOVA) with the factors Delay (short and long) and Task (A and B). We analyzed PE with $\chi^2$ tests. We will only report effects that were statistically significant (with error criterion $P<0.05$). We define the benefit of preparation in RT as *mean RT in the short delay condition – mean RT in the long delay condition*. Similarly, the benefit of preparation in PE is defined as *PE in the short delay condition – PE in the long delay condition*.

In the RT data of monkey 1, there was a significant benefit of long preparation time (42 ms), as indicated by the main effect of Delay [$F(1,715)=157.5$, $P<0.001$]. Responses in task B were 22 ms faster than in task A, as shown by the main effect of task [$F(1,715)=166.1$, $P<0.001$]. The benefit of longer advance preparation time was 32 ms and 52 ms in tasks A and B, respectively, as revealed by the significant interaction between the factors Task and Delay [$F(1,715)=7.5$, $P<0.01$].

The $\chi^2$ analysis of the error data showed that there were significantly more errors in the short (11.2%) than in the long (3.4%) delay condition [$\chi^2$ (1)=17.2, $P<0.001$].

The data of monkey 2 were similar to the data of monkey 1. There was a significant benefit (6 ms) of long preparation time, as indicated by the main effect of Delay [$F(1,1183)=11.2$, $P<0.001$]. The effect of Task [$F(1,1183)=142.1$, $P<0.001$] indicated that responses in task B were 18 ms faster than in task A. The benefit of task preparation was task specific (9 ms in task A and 1 ms in task B),
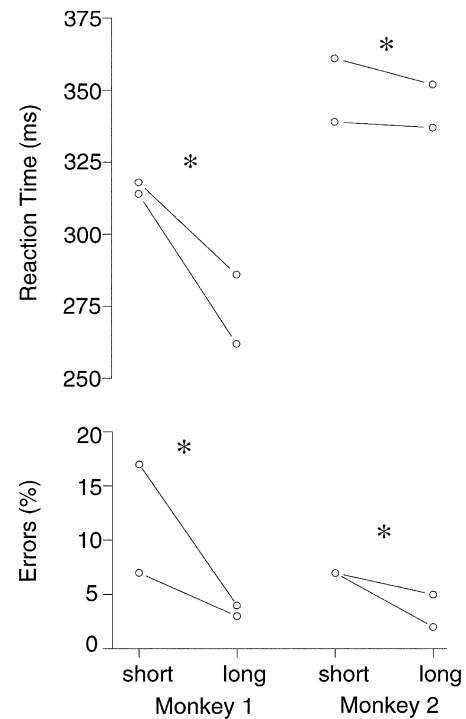


**Fig. 3** Mean RT and percentage of errors (PE) as a function of task type (A versus B) and Delay (short versus long). *Circles* indicate the mean. Error bars would be smaller than the plotting symbols and are therefore not shown (SEM<6 ms). Reaction time and PE were significantly decreased with longer preparation time in both monkeys and in both tasks (negative slope of all 8 lines; *asterisk* indicates that the effect is statistically significant). The interaction between preparation interval and task was significant in RT for both monkeys (lines are not parallel). This indicates that the processing that occurred during the preparation interval was task specific

as shown by the significant interaction between Delay and Task [$F(1,1183)=5.6$, $P<0.05$].

The $\chi^2$ analysis of the error data showed that there were significantly more errors in the short (7.0%) than in the long (3.8%) delay condition [$\chi^2$ (1)=5.5, $P<0.05$].

Altogether, both monkeys performed better with the longer delay. There was an interaction between the factors Task and Delay. Task preparation would likely require different amounts of time for the two different tasks, resulting in exactly such an interaction. Task cue memorization, on the other hand, would likely require similar amounts of time for the two different cues, and therefore would not result in an interaction between Task and Delay. Similarly, any non-specific effect of the delay would be likely to have a similar influence on the two tasks, and so would also not result in an interaction between Task and Delay. Thus, the presence of an interaction supports a task-specific preparation strategy, and not a memorization strategy.

Although there was a clear task-specific benefit of longer delays for both animals, the pattern of those benefits were reversed in monkeys 1 and 2 (Fig. 3). For monkey 1, task B benefited more than task A (steeper lines connect the task B data points than the task A data points for RT), while the reverse is true for monkey 2. However,
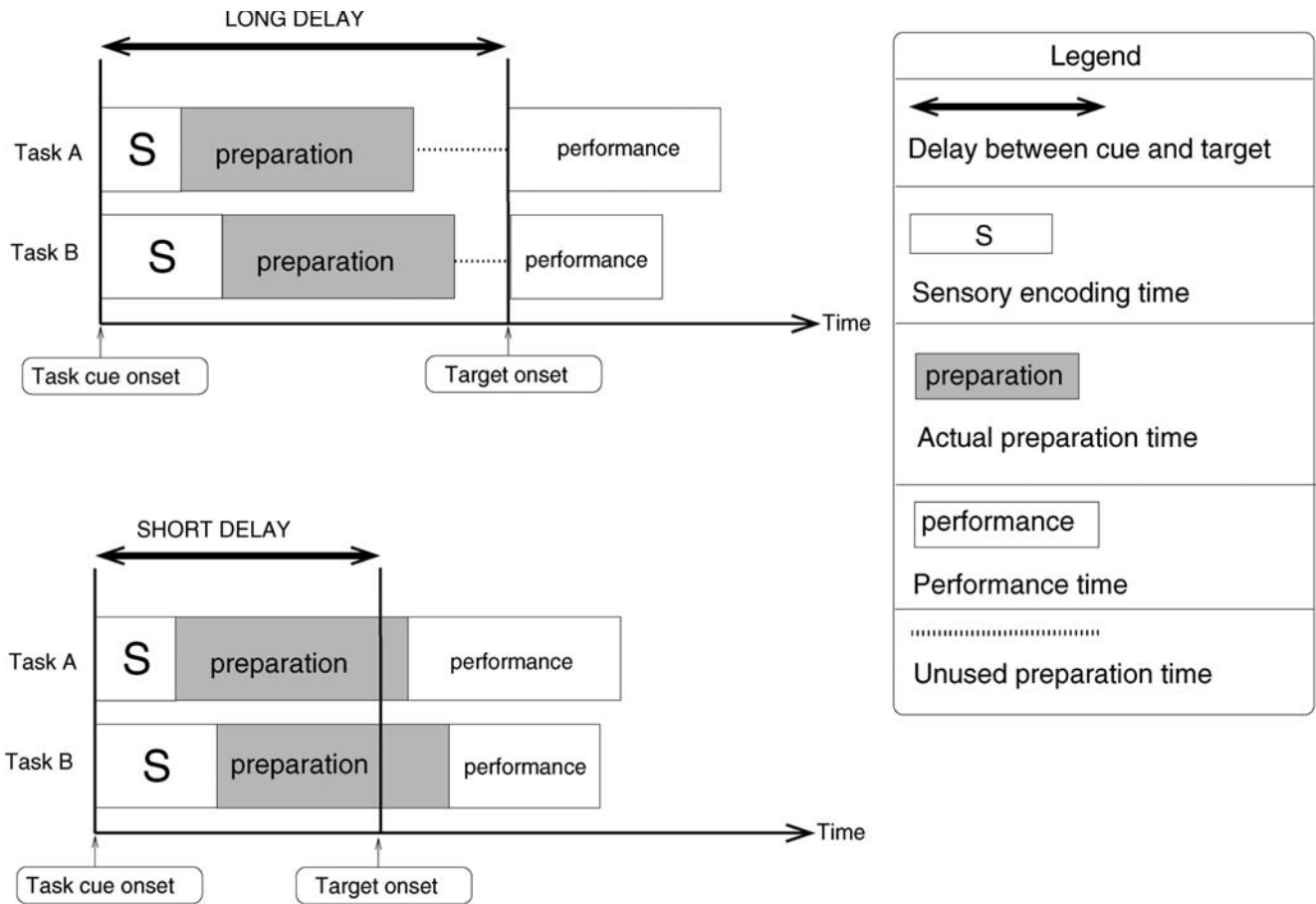
**Fig. 4** Enhanced model of information processing during the task-switching paradigm. Similar to Fig. 2, but with an additional stage for encoding the sensory cue (*S*). If *S* is different for tasks A and B, then there will be an interaction between the factors Task and Delay, even if the actual preparation times (*grey boxes*) are equal for both tasks (as illustrated). Thus, differences in sensory encoding alone can lead to the same predictions as the model illustrated in Fig. 2, in which it was assumed that sensory encoding is equal among task conditions. Experiment 2 tests whether the findings of experiment 1 could be due to differences in sensory encoding time *S* rather than due to differences in preparation time

the particular tasks were different in the two animals, and therefore this difference has no bearing on our findings. The important point is that, in both animals, performance improved with longer delays, and this improvement was task specific, consistent with an advance preparation strategy.

## Experiment 2

In our stage model of the task-switching paradigm (Fig. 2), we assumed that identification of the two different task cues (yellow and blue backgrounds) consumed equal amounts of time. If this is not the case, then the finding of a task-specific effect of changing delay no longer unequivocally supports the use of the advance preparation strategy. Instead, a short delay may allow enough time for task cue

encoding in one task but not in the other, leading to a longer response time in just one task. This differential lag would not occur with a long delay (Fig. 4). Therefore, we tested whether task-specific effects of changing the delay time might be due to different times required for sensory processing. Only by ruling out this possibility can we conclude that monkeys are able to prepare tasks in advance.

The most straightforward way to determine the sensory processing times of the cues would be to train the subjects on a color discrimination task. Response times for yellow and blue stimuli could then be directly compared. Unfortunately, such a task might interfere with performance in the task-switching paradigm, in which yellow and blue serve as task cues. To avoid confusing the animals, we chose two alternative ways to establish the contribution of sensory processing times to the overall RT. We modified the brightness levels of the task cues for monkey 1 and we replaced the color task cues with oriented triangles for monkey 2. If sensory processing times are different for different types of cues, and if these differences account for the task-specific effects that we observe, then modifying the physical properties of the cues should change the pattern of task-specific effects. If, however, sensory processing times are relatively similar for the different task cues, a change in physical properties should not change the pattern. We tested both monkeys on the same paradigm, but now with different sets of cues. We will refer to the second set of cues as cue-set 2.

## Methods

### *Subjects*

Same as in experiment 1.

### *Apparatus and stimuli*

We used the same equipment as for experiment 1. Stimuli were different. For monkey 1, apart from the brightness of the task cues, all stimulus features were as before. Originally, the brightness of the yellow and blue task cues were 0.03 cd/m$^2$ and 0.10 cd/m$^2$, respectively, as measured with a Tektronix J17 Luma Color photometer. Now the brightness order was reversed: yellow and blue task cues were 0.11 cd/m$^2$ and 0.01 cd/m$^2$, respectively.

For monkey 2 we used equilateral (14.7°) grey triangles, which pointed either up (task A) or down (task B). We used longer delays (220 and 610 ms for short and long, respectively). Longer times were necessary in order to achieve performance comparable to that of using colored task cues.

### *Design and procedure*

Same as in experiment 1.

### Results and discussion

In the RT data of monkey 1 (Fig. 5), there was a benefit of preparation of 49 ms, as revealed by the significant effect of Delay [$F(1,1407)=884.0$, $P<0.001$]. The main effect of Task indicated that task B was performed 20 ms faster than task A [$F(1,1407)=337.7$, $P<0.001$]. The interaction between Task and Delay [$F(1,1407)=12.5$, $P<0.001$] showed that the effect of advance preparation was task dependent. The benefit of long preparation was 44 ms in task A and 55 ms in task B.

We also found a benefit of preparation in the error data of 13% [effect of Delay was significant, $\chi^2 (1)=105.6$, $P<0.001$]. Task B was performed more accurately than task A (benefit of 2.2%), as revealed by the effect of Task [$\chi^2 (1)=4.3$, $P<0.05$]. The interaction between Delay and Task [$\chi^2 (3)=11.6$, $P<0.001$] shows that the benefit of preparation was task specific (20% and 4% in tasks A and B, respectively).

In the RT data of monkey 2 (Fig. 5), we found a significant main effect of Delay [$F(1,1127)=88.8$, $P < 0.001$], showing a benefit of preparation of 18 ms. We found a significant main effect of Task [$F(1,1127)=174.8$, $P<0.001$], indicating an advantage of task B over task A of 25 ms. There was a significant interaction between Task and Delay [$F(1,1127)=21.8$, $P<0.001$], revealing a task specific benefit of preparation (27 ms in task A and 9 ms in B). There were no significant effects in the error data.

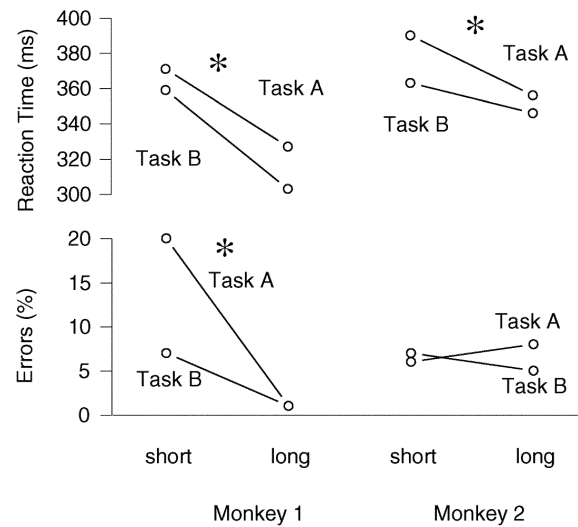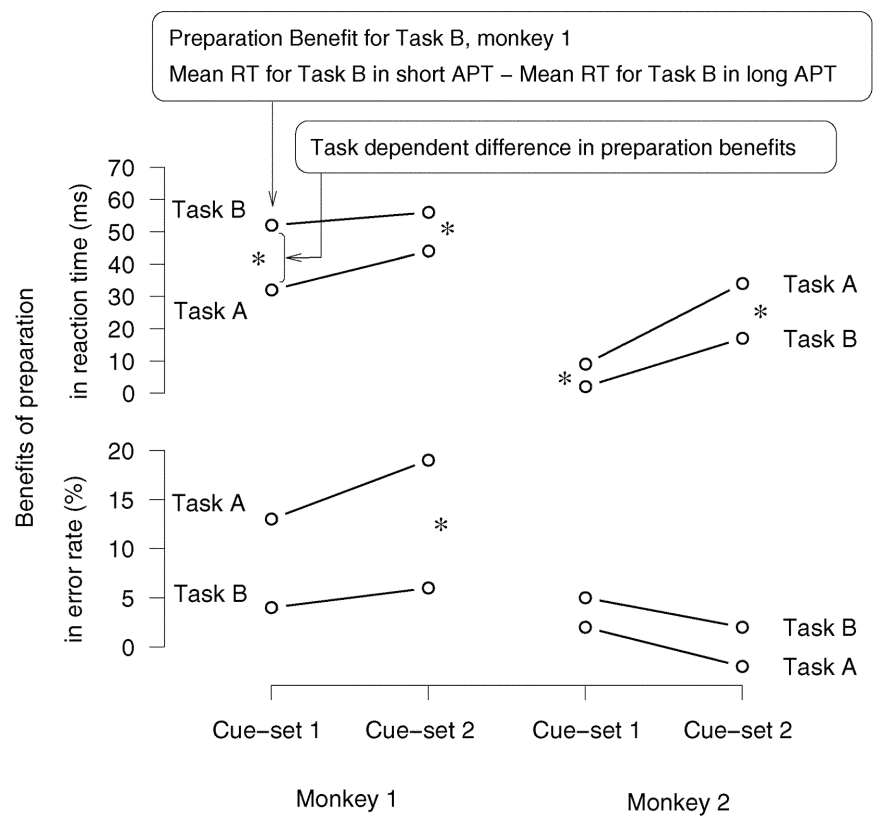In Fig. 6 we show the benefit of longer preparation times for both tasks and both cue-sets (i.e., results from experiments 1 and 2 combined). The data points in this figure represent the mean benefit of longer preparation time. Despite the physical differences of the task cues, the relative relationship between the benefits in the two tasks is the same for both cue-sets and for both monkeys. (This can be seen by the fact that in no case do the task A and task B lines cross one another). This indicates that the task specific benefits of task type are better explained by differences in advance preparation rather than by differences in the physical properties of the cues.

## General discussion

The current results provide evidence that monkeys are able to prepare tasks in advance in an abstract way. Monkeys responded to a target in accordance with a previously cued task. Responses were faster when the animals were given more time to prepare the task, that is, when there was a longer delay between the task cue and the target. The benefit of longer preparation time was different for the two tasks that each monkey performed. Thus, the benefit of longer preparation time was task specific.

The fact that the benefit of longer preparation time is task-specific is critical for showing that monkeys can prepare a task in advance when only abstract information is available. In humans, we rely on introspection to tell us that we prepare tasks in advance. In monkeys, hard evidence is required. Merely showing a benefit of longer cue-target intervals is not sufficient. For example, allowing a subject more time to perceive which task cue has been presented can result in a benefit that is unrelated to



**Fig. 5** Mean RT and PE as a function of task type and advance preparation interval with altered task cues. *Circles* indicate the mean. Error bars would be smaller than the plotting symbols (<3 ms). Results are similar for both sets of cues. RT and PE decreased with longer preparation time (*asterisk* indicates statistical significance), and the interaction between preparation time and task was significant, indicating that the benefit of preparation time was task-dependent

**Fig. 6** Benefits of long versus short delay in RT and PE. Data are shown for each monkey, task type and cue-set. The benefit of a long delay was task-specific for RT under all four conditions, and in PE for one of the four (*asterisk*). In no case did a change in the cue-set alter the pattern of this task-specific benefit. For example, monkey 1 showed a greater benefit of advance preparation in task B than in task A (task B RT data point above task A data point) when tested using either cue-set 1 or cue-set 2. A reversal of the pattern of benefits would result in the task A and task B lines crossing. Such a crossing did not occur in either animal in the RT or in the PE data. This strongly suggests that the task-specific benefit was not a result of one cue requiring more time to process than the other. If this were the case, then changing the cue-set would be likely to change the pattern of benefits. Instead, task-specific benefits occurred because of differences in advance task preparation



advance task preparation. However, the finding of a *task-specific* benefit of increased preparation time is good evidence that monkeys actually use the task cue in order to actively prepare the upcoming task.

Previous work in macaque monkeys has shown that animals can learn to respond to similar targets in different ways. For example, monkeys can be trained to make an eye movement to a peripheral target as soon as it appears, or to withhold the movement until a particular signal is given. Animals can switch back and forth between performing the two different behaviors. However, no advance preparation occurs. Instead, animals learn to switch from one task state to another in response to not being rewarded for a particular behavior (e.g., Bushnell et al. 1981) or in response to instructional trials in which the stimuli are markedly changed (e.g., Eskandar and Assad 1999). In other studies, animals have been trained to apply one of two different rules to a stimulus; for example, "match/no-match" (Wallis et al. 2001). In these cases, however, there is no behavioral evidence that advance preparation occurs. In theory, animals could solve such tasks by merely storing the task cue, and waiting until the imperative stimulus appears before actually interpreting the cue.

Neurophysiological experiments have provided the best evidence for advance task preparation, but this evidence has not been conclusive. A simple case of advance task preparation occurs in the premotor cortex, where activity is correlated with a particular upcoming movement (Wise et al. 1983). This is referred to as "motor set." A similar activity can be found in the PPC, where many neurons are activated specifically during the preparation of either an upcoming eye or arm movement (Snyder et al. 1997). Because the PPC is not generally considered a premotor structure, these signals have been referred to as "motor intention" rather than "motor set" (Mazzoni et al. 1996). However, these examples of advance planning fall short of the ability to instantiate a particular sensory-motor mapping prior to receipt of the imperative stimulus. Instead, they merely reflect the animal's ability to plan a fully specified action in advance.

It has recently been shown that motor intention signals can occur in the PPC even in the complete absence of a spatial goal (Calton et al. 2002). Neurons in the parietal reach region reflect the plan to make an arm movement to the very next target to appear, while neurons in the lateral intraparietal area reflect the plan to make an eye movement to the very next target to appear. These intention activities are not merely memories of the instructions themselves, since they occur in locations that have previously been shown to be specifically related to either eye or arm movements (Snyder et al. 1997). Thus, this non-spatial intention activity is abstracted both from the particular instruction as well as from any specific motor plan. Here again, however, a neural correlate of the animal's ability to plan a partially specified action in advance falls short of the ability to instantiate a particular sensory-motor mapping in advance.

Two studies have demonstrated that neuronal activity in the dorsal lateral prefrontal cortex is correlated with a

particular abstract task rule (Asaad et al. 2000; Wallis et al. 2001). The study by Wallis and colleagues is especially relevant. Monkeys were presented with a sample stimulus and instructed to perform either a match to sample task or a non-match to sample task. In the interval prior to seeing the potential match target, the activity of many cells was correlated with the particular rule (match or non-match) that had been instructed. This correlation occurred when the rule was cued using either of two very different cue sets. Thus, these neurons encode an abstract task rule, at least when presented in conjunction with a particular stimulus. However, this study still leaves open whether or not the animals derived any benefit from this encoding. It is unclear whether this activity reflects a process by which animals actively prepare for an upcoming task, in such a way as to gain an advantage compared to a state in which they have not prepared.

Until now we have avoided any specific mechanistic interpretations of our findings, and instead have used only the generic term "advance preparation" to describe what we believe our results indicate. Our study was designed to determine whether or not some form of abstract task preparation occurred, and not to characterize that preparation. The data do allow us, however, to argue against non-specific mechanisms as the source of the improvement in performance. For example, one might imagine that longer preparation periods allow a build-up analogous to the progressive compression of a spring – the longer the interval until release, the faster the response. By definition, however, a non-specific mechanism would not be expected to result in a relative difference in performance on the difference tasks. A similar argument applies to the idea that longer delay periods may reduce interference between the instructional cue and the stimulus.

The current study provides evidence that monkeys do in fact derive a benefit from a longer delay between task instruction and target stimulus. Since this benefit is task dependent in both monkeys, we conclude that they are able to prepare tasks in advance. Much human behavior depends critically on just this ability. An exciting question is where and how task encoding is implemented in the brain. The single unit studies just described have implicated the dorsolateral prefrontal cortex. Brain imaging studies in humans have suggested that not only the prefrontal but also posterior parietal areas are active during task preparation (Dove et al. 2000; Pollmann et al. 2000; Sohn et al. 2000). We believe that chronometric behavioral data of the sort described in the current study, in conjunction with single unit recording, will be instrumental in elucidating the relative roles of parietal and frontal areas in advance task preparation.

# References

Asaad WF, Rainer G, Miller EK (2000) Task-specific neural activity in the primate prefrontal cortex. J Neurophysiol 84:451–459

Bushnell MC, Goldberg ME, Robinson DL (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. J Neurophysiol 46:755–772

Calton JL, Dickinson AR, Snyder LH (2002) Non-spatial, motor-specific activation in posterior parietal cortex. Nat Neurosci 5:580–588

Cherkasova MV, Manoach DS, Intriligator JM, Barton JJS (2002) Antisaccades and task-switching: interactions in controlled processing. Exp Brain Res 144:528–537

Cook EP, Maunsell JH (2002) Dynamics of neuronal responses in macaque mt and vip during motion detection. Nat Neurosci 5:985–994

Dove A, Pollmann S, Schubert T, Wiggins CJ, von Cramon DY (2000) Prefrontal cortex activation in task shifting: an event-related fMRI study. Cogn Brain Res 9:103–109

Eskandar EN, Assad JA (1999) Dissociation of visual, motor and predictive signals in parietal cortex during visual guidance. Nat Neurosci 2:88–93

Gilbert SJ, Shallice T (2002) Task switching: a PDP model. Cogn Psychol 44:297–337

Kavcic V, Krar FJ, Doty RW (1999) Temporal cost of switching between kinds of visual stimuli in a memory task. Cogn Brain Res 9:199–203

Konishi S, Hayashi T, Uchida I, Kikyo H, Takahashi E, Miyashita Y (2002) Hemispheric asymmetry in human lateral prefrontal cortex during cognitive set shifting. Proc Natl Acad Sci USA 99:7803–7808

Kramer AF, Hahn S, Gopher D (1999) Task coordination and aging: exploration of executive control processes in the task switching paradigm. Acta Psychol 101:339–378

Le TH, Pardo JV, Hu X (1998) 4 T-fMRI study of nonspatial shifting of selective attention: cerebellar and parietal contributions. J Neurophysiol 79:1535–1548

Mazzoni P, Bracewell RM, Barash S, Anderson RA (1996) Motor intention in the macaque's lateral intraparietal area. I. Dissociation of motor plan from sensory memory. J Neurophysiol 76:1439–1456

Meiran N (1996) Reconfiguration of processing mode prior to task performance. J Exp Psychol Learn Mem Cogn 22:1423–1442

Moulden DJA, Pioton TW, Meiran N, Stuss DT, Riera JJ, Valdes-Sosa P (1998) Event-related potentials when switching attention between task-sets. Brain Cogn 37:186–190

Pietrewicz AT, Kamil AC (1979) Search image formation in the blue jay (*Cyanocitta cristata*). Science 204:1332–1333

Pollmann S, Dove A, von Cramon DY, Wiggins CJ (2000) Event-related fMRI: comparison of conditions with varying BOLD overlap. Hum Brain Mapping 9:26–37

Rainer G, Rao SC, Miller EK (1999) Prospective coding for objects in primate prefrontal cortex. J Neurosci 19:5493–5505

Reid JP, Shettleworth SJ (1992) Detection of cryptic prey: search image or search rate? J Exp Psychol Anim Behav Process 18:273–286

Rogers RD, Monsell S (1995) Cost of a predictable switch between simple cognitive tasks. J Exp Psychol Hum Percept Perform 124:207–231

Snyder LH, Batista AP, Andersen RA (1997) Coding of intention in the posterior parietal cortex. Nature 386:167–170

Sohn M, Ursu S, Anderson JR, Stenger VA, Carter CS (2000) The role of prefrontal cortex and posterior parietal cortex in task switching. Proc Natl Acad Sci USA 97:13448–13453

Sternberg S (1969) The discovery of processing stages: extensions of donders' method. In: Koster WG (ed) Attention and performance II, North Holland, Amsterdam, pp 276–315

Sternberg S (2001) Separate modifiability, mental modules, and the use of pure and composite measures to reveal them. Acta Psychol 106:147–246

Stoet G, Snyder LH (2003) Executive control and task-switching in monkeys. Neuropsychologia (in press)

Vandierendonck A (2000) Executive functions and task switching. Psychol Belg 40:211–226

Wallis JD, Anderson KC, Miller EK (2001) Single neurons in prefrontal cortex encode abstract rules. Nature 411:953–956

Wise SP, Weinrich M, Mauritz KH (1983) Motor aspects of cue-related neuronal activity in premotor cortex of the rhesus monkey. Brain Res 260:301–305

Wylie G, Allport A (2000) Task switching and the measurement of "switch costs." Psychol Res 63:212–233