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## **TASK-SWITCHING**

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## Task-Switching in Human and Nonhuman Primates: Understanding Rule Encoding and Control from Behavior to Single Neurons

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Task-switching paradigms are a favorite choice for studying how humans represent and apply rules. These paradigms consist of trials of two different task contexts, each with its own rules, between which subjects frequently switch. Measuring the difficulty subjects have when switching between tasks taps into a fundamental property of executive control, that is, the capacity to respond to stimuli according to task context.

Although any biological organism can have a fixed response to sensory inputs, it is nontrivial to process identical inputs in different ways, depending on the task context. Task-switching paradigms are designed to study how subjects respond in the face of changing task contexts. In the last decade, more than 400 studies using this paradigm have been published (for an overview, see Monsell, 2003). Most of these studies are about human task-switching. However, unfortunately, there are limits to what we can learn from humans. We can look at behavior, and at regional brain metabolism, but it is very difficult to study the individual neuronal level using invasive techniques. In this chapter, we use rhesus monkeys as a model system to look at executive control at the neuronal level. A large number of studies have done something similar in the frontal lobes (e.g., see Chapters 9, 10, 11, and 13). We concentrate on the parietal lobe, and show that parietal neurons play a critical role in executive control. The idea that the parietal lobe might play a role in executive control is surprising, but not altogether unanticipated. After all, the posterior parietal cortex (PPC) is an association area, and thus a likely candidate for integrating different cortical processes. A number of brain imaging studies have focused on executive functions in the parietal cortex (e.g., Sohn et al., 2000; Rushworth et al., 2001; Gurd et al., 2002; Sylvester et al., 2003), and several recent studies in monkeys demonstrated the integration between top-down and bottom-up information (e.g., Chafee and Goldman-Rakic, 2000). We hypothesize that the complex set of general functions necessary for controlling mental functions is

distributed over a large area of the brain, rather than being limited to just one region or lobe of the brain.

Before we address any of the questions regarding neural activity, we will first ask whether monkeys and humans behave similarly in their deployment of executive processes. This is an interesting question because executive control in a human appears to be quite sophisticated. A rhesus monkey might not have available the full range of human executive functions and therefore might perform quite differently from a human in a task-switching paradigm. Therefore, we will first ask whether it is the case that humans have evolved to be particularly good at processing information in different ways and in rapidly switching their processing in response to changes in the task context. We will show that this is not the case; what humans are good at, compared with monkeys, is not switching between two tasks, but rather, locking on to a single task.

### THE TASK-SWITCHING PARADIGM

In a task-switching paradigm, subjects perform interleaved trials of two or more different tasks in rapid succession. There are different types of task-switching paradigms. In uncued task-switching paradigms, subjects know through an instruction when to perform what task. For example, in the alternating-runs paradigm of Rogers and Monsell (1995), subjects know that they have to switch tasks every two trials. A disadvantage of this paradigm is that it is impossible to determine when subjects start to prepare for an upcoming task switch. This problem is solved in cued task-switching paradigms, in which each trial begins with the presentation of a task instruction cue. This cue indicates the rule that must be applied to the subsequent imperative stimulus. For example, in a switch paradigm in which the imperative stimulus is a number, one cue might instruct the subject to determine whether the number is even, whereas another cue might instruct the subject to determine whether the number is greater than 5. With randomly interleaved tasks in a cued task-switching paradigm, subjects cannot reliably prepare the upcoming task until the task cue has been presented. If the purpose of an experiment is to measure neural correlates of task preparation or rule application, it is an advantage to be able to determine exactly when the preparation process starts.

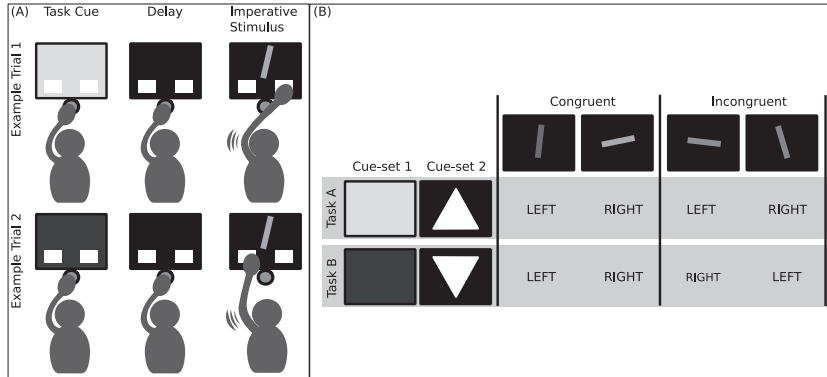
Finally, a very different type of task-switching paradigm is the Wisconsin Card Sorting Task (WCST), in which subjects sort cards according to a rule that is based on either the color or the symbols on the cards. After a fixed number of consecutive successful trials, the experimenter changes the sorting rule. This change results in sorting errors, and the subject must use error feedback to learn the new rule. One measure of executive control in this test is the number of trials required for a subject to learn a new rule. Perseveration on the old rule is taken as an indication of executive impairment, and is seen in various frontal brain syndromes (Sullivan et al., 1993). Although the WCST has been used for decades to diagnose cognitive impairment, computerized variations have been used in studying executive control and rule representation in animals

(Dias et al., 1996; Mansouri and Tanaka, 2002; Rushworth et al., 2002; Everling and DeSouza, 2005). The WCST has a similar problem to the alternating-runs paradigm. Because rule switches are unannounced and have to be discovered by the subjects themselves, the time at which the subject switches from preparing one task to preparing another task is ambiguous. Thus, although the WCST is useful for studying how long it takes subjects to discover a change in the task, the processes that underlie switching to apply a new set of task rules are more difficult to pin down.

Task-switching paradigms provide two independent measures of task-switching performance: switch costs and incongruity costs. The subject's ability to switch from one task to another is quantified by subtracting the performance (e.g., response time) in task-repetition trials from the performance in task-switching trials. The subject's ability to ignore distracting, irrelevant information is assessed by subtracting the performance in trials using a stimulus that instructs the same response on each task (an example of a congruent stimulus in the aforementioned example task is the digit "7," which is both odd and greater than 5) from performance in trials using a stimulus that instructs different responses (an incongruent stimulus) [e.g., the digit "3," which is odd, but not greater than 5]. To compare monkey and human behavior in task-switching, we needed to develop a version of the task that could be performed by both species. Instead of using letters and numbers, as is common in human task-switching experiments, we used shapes or colors, rather than verbal instructions, to cue the two different tasks, and we made the tasks themselves concrete (based on simple, observable properties of the stimuli).

Two monkeys (*Macaca mulatta*) [M1 and M2] and seven human volunteers (H1–H7) were compared using the same experimental setup. At the beginning of each trial, subjects were informed by a yellow or blue screen, or by an upright or inverted triangle, which of two tasks was to be performed. After a short preparatory delay, an imperative stimulus appeared. For half of the subjects, this stimulus was a square; for the other half of the subjects, this stimulus was a line. In task A, the subjects had to judge whether the color of the imperative stimulus (the square or the line) was closer to red or to green. In task B, subjects M1 and H1–H4 had to judge whether the inside of the square was more or less bright than the outer border of the square, and subjects M2 and H5–H7 had to judge whether the line orientation was horizontal or vertical (Fig. 11–1; see color insert). Subjects pressed a left or right response button to indicate their judgment.

Stimuli were presented on a touch-sensitive video screen located just in front of the subject. Subjects began each trial by holding a home key, and then responded to the imperative stimulus by moving to touch one of two white squares positioned at the left and right bottom portions of the screen. Target color was randomly chosen from a large number of different shades of red and green (e.g., pink, orange, cyan). For square stimuli (the first half of the subjects), the luminances of the border and inside regions were similarly chosen from a wide range of possible values. The different combinations of color and luminance contrasts yielded 104 different target stimuli. For lines (the second



**Figure 11-1** Experimental paradigm and stimulus response associations. *A.* Two example trials. The monkey (or human) sits behind a touch-sensitive screen and the hand is positioned in resting position on the *orange* home key. Each trial started with a 250-ms task cue indicating which of two task rules to apply to the subsequent stimulus. The task was cued by either a color (*blue* or *yellow*) or a shape (*upright* or *inverted triangle*). After a 190- to 485-ms delay period, the imperative stimulus, a *colored, oriented bar*, appeared. Depending on the task rule, either the color or the orientation of the stimulus was relevant. In the color discrimination task (example trial 1), or task A, *red* stimuli required a left button press and *green* stimuli required a right button press. In the orientation discrimination task (example trial 2), or task B, *vertical bars* required a left button press and *horizontal bars* required a right button press. Liquid rewards followed correct responses for monkeys. *B.* Stimulus-response combinations. One of two possible cues was used to indicate task A or task B. A single set of imperative stimuli was used in both tasks. Congruent stimuli were mapped to the same response button in both tasks, whereas incongruent stimuli were mapped to opposite buttons.

half of the subjects), orientation was graded, but limited to within 10 degrees of horizontal or vertical. The large range of color and luminance, or color and orientation, was chosen to encourage the use of general rules rather than a memory-based strategy for solving the tasks. A memory-based strategy might, for example, involve memorizing every possible cue-response pair, along with its correct response. In this undesirable scenario, animals might perform the task using associative recall, rather than performing one of two different discrimination tasks. The use of two different stimulus shapes (lines or squares), two different sets of task cues (triangles or screen color), and two different second tasks (orientation or luminance gradient) were all intended to help to establish the generality of our results.

Animals were first trained on a single task. Once proficient, they were trained on a second task. When they learned the second task, they were switched back to the first task, which had to be relearned. This process of switching continued, with switches occurring ever more frequently, until the two tasks were completely and randomly interleaved.

Each trial started when the subject put its dominant hand on the home key (Fig. 11–1A). The response buttons appeared immediately and remained on until the end of the trial. Next, the task cue appeared (250 ms), followed by a blank screen (500–600 ms). Then the imperative stimulus appeared and remained on-screen until the subject released the home key. The subject then had 2000 ms to move to within approximately 6 cm of the left or right response button. The behavioral reaction time (RT) was measured as the interval between onset of the imperative stimulus and release of the home key. Monkeys were rewarded for correct responses with a drop of water; humans were not rewarded. Incorrect trials for both species were followed by a visual error signal and a 1-s time-out period.

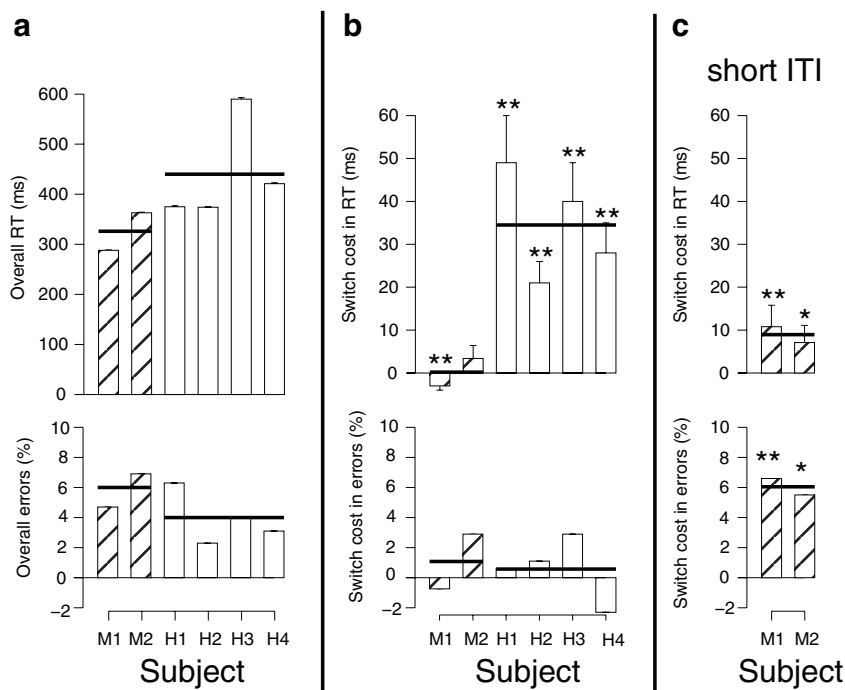
We recorded eye movements using the scleral search coil technique. The data show that monkeys typically kept their eyes at the center of the screen and made a saccade to the response button shortly before moving their arm.

For the monkeys and for three of the seven humans, the task cue was present for only the first 200 ms of the task preparation interval. This was intended to encourage the subjects to actively process the task cue before receiving the imperative stimulus. An analysis of the data obtained with variable preparatory intervals demonstrated that this was, in fact, the case (Stoet and Snyder, 2003). For the first four humans tested, the task cue remained on-screen throughout the task preparation interval, making the task slightly easier. In these first four human subjects, the intertrial interval (ITI) was shorter than that used with the monkeys and with the final three humans (250 ms versus 345 ms). The shorter ITI compensated for the quicker responses to target stimuli in the monkey subjects. See Meiran (1996) for a discussion of the effects of ITIs on human switch costs. 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 of humans (H1–H4).

## COMPARISON OF MONKEY AND HUMAN TASK-SWITCHING

We first compared the behavioral performance of monkeys and humans during task-switching. To use monkey task-switching as a model system to study human cognition processing, it is not necessary that monkeys perform identically to humans. However, it is crucial to have a good understanding of any differences that might exist.

We assessed switch costs after monkeys and humans were trained to comparable success rates. We analyzed RTs using analysis of variance with the factors “switch” and “congruency.” For this data analysis, we excluded all error trials and trials that immediately followed an error trial. We analyzed the percentage of errors (PE) with chi-square tests. When computed across all trials, performance was similar for the two species (Fig. 11–2A). 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 average, humans were slightly more accurate than monkeys (mean PE = 3.9% versus 5.8%).



**Figure 11–2** Humans show switch costs, but monkeys do not. *A*. Overall performance by monkeys (M1 and M2) [shaded bars] and human subjects (H1–H4) [open bars]. Monkeys showed a faster reaction time (RT) [top], but had similar accuracy, as measured by percentage of errors (PE) [bottom]. Horizontal lines show species means. Error bars show standard error of the mean for RT. *B*. Switch costs in RT (mean RT on switch trials minus mean RT in repetition trials,  $\pm$ standard error of the mean) and PE (PE on switch trials minus PE in repetition trials) in monkeys and humans. Only humans showed significant switch costs in RT (assessed using analysis of variance,  $**p < 0.01$ ,  $*p < 0.05$ ). 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. *C*. Switch costs appeared in monkeys when short intertrial intervals (ITI) were used (170 ms).

Despite their similarity in overall RT and error rate, humans and monkeys show a striking difference in their ability to switch from one task to another. Human RTs were significantly slowed in the trial immediately after a task switch (Fig. 11–2*B*). Switch costs in response times were large and highly significant for each of the four human subjects ( $p < 0.01$ ). Costs ranged from 21–49 ms and had a mean value of 35 ms. Results were similar in the second set of subjects (costs ranged from 20–49 ms, with a mean switch cost of 31 ms in RT). In contrast, neither monkey showed a significant switch cost, in either RT (mean cost = 0.2 ms) or PE (mean cost = 1%). Monkey 1 had a small, but significant



( $p < 0.01$ ) negative switch cost in the original experiments, but we were unable to reproduce this effect on subsequent testing; therefore, we believe it to be a false-positive finding.

Switch costs may arise in at least two ways: (1) There may be task inertia, that is, a lingering representation of the previous task set that inhibits the installation of a new task set (Allport et al., 1994). (2) 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 believed to contribute to human switch costs (Allport et al., 1994; Meiran, 1996). Evidence for the role of task inertia is provided by the decrease in human switch costs with increasing preparation time, as if the effect of the previous task wears off over time (Meiran, 1996). However, even with long preparation or ITIs (e.g., 1.6 s), 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 off, suggests that the installation of the new task remains incomplete until a new stimulus actually arrives (Rogers and Monsell, 1995; Meiran, 1996).

The absence of residual switch costs in monkeys suggests that, in monkeys, unlike in humans, neural circuits can be completely reconfigured to perform a new task before 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. 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) ITIs. We found significant switch costs in both monkeys in the short ITI blocks (11 ms and 7 ms in RT; 6.6% and 5.5% in PE, all measures different from zero at  $p < 0.05$ ) [Fig. 11–2C]. 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.

Task-switching 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 at hand is the ability to attend only to those stimulus features that are relevant, and to ignore those that are irrelevant. Incongruency costs measure the extent to which a subject fails in this ability. As illustrated in Figure 11–2, both animals showed clear incongruency costs in RT (9 ms 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: Incongruency costs in both RT (33 ms and 28 ms) and PE (9.2% and 11.8%) were both highly significant (Fig 11–2C).

The higher incongruency costs in monkeys suggest one possible reason that monkeys, unlike humans, do not show switch costs: They are not as focused on the relevant features of the task in the first place. There are several other potential explanations for why the monkeys do not show persistent switch costs. For example, animals might use an approach that circumvents the need to change strategies between the two tasks. One way to do this would be to memorize every possible cue-target response triplet. We intentionally used a wide range of target stimuli to promote the use of a rule-based rather than memory-based strategy. However, it is nonetheless conceivable that monkeys memorized all 208 combinations and employ a memory-based strategy to solve the task. To distinguish between these two strategies, we used a probe task that introduced 11 novel stimuli to monkey M2, interspersed with the practiced target stimuli. The novel stimuli were created using various combinations of a previously unseen line orientation (20 or 45 degrees from either the horizontal or vertical axis), a new color (blue-gray), or a new line thickness (1.1 degree). Combinations of novel features were chosen such that the task-relevant stimulus dimension was unambiguous in the task context, even though some features of the novel stimuli were ambiguous (e.g., blue-gray color, 45-degree orientation). For example, a novel stimulus consisting of a 45-degree red line in the context of task A would instruct the animal to move left. Each novel stimulus was presented only once, after the animal was extremely well practiced on two tasks using the standard stimuli. If the monkey learned specific cue-target-response combinations rather than general rules, then it should have performed at chance levels on the novel stimuli. Instead, performance was correct for 10 of the 11 novel stimuli (90% success rate). This is significantly greater than chance (chi square [1] = 7.4,  $p < 0.01$ ), indicating that the animal had learned to apply general rules and was not using a memory-based strategy to solve the task.

### NEURAL ENCODING OF TASK RULES

The task-switching paradigm provides an opportunity to study the neural instantiation of rules, despite the fact that monkeys do not show persistent switch costs. Behavioral evidence demonstrates that monkeys prepare each task in advance, processing whichever rule has been cued in advance of seeing the imperative stimulus: Monkeys perform faster and more accurately in the task-switching paradigm when there are longer delays between the task cue and the imperative stimulus (Stoet and Snyder, 2003). By comparing neural activity during the preparation periods of two different tasks, we can therefore determine whether and how a particular neuronal population encodes task rules. The particular advantage of the task-switching paradigm for this purpose is that, by comparing activity during the preparation period for the two tasks before the appearance of the imperative stimulus, everything but the rule itself is completely controlled for. Thus, any differential activity that occurs during the preparatory period for the two tasks can be unambiguously assigned to

the processing of the rules themselves. In this section, we apply this method to investigate neurons in the monkey PPC.

We recorded data from 378 isolated neurons in and around the right intraparietal sulcus (IPS) of the right PPC of two animals. We tested for task-rule selectivity by comparing the final 150 or 250 ms of delay-period activity in trials starting with yellow versus blue task cues (Student's *t*-test). Twenty-nine percent of neurons ( $n = 111$ ) showed a significant difference in activity, depending on which task was being prepared.

We projected each recording site location onto an anatomical magnetic resonance image of the cortex to determine which cortical areas the neurons belonged to (see Fig. 11–3; see color insert). Neurons that were selective for one particular task rule over the other (henceforth called task-positive, or TASK<sup>+</sup>, cells) were located primarily on the lateral bank of the IPS and the adjacent gyral surface (including areas LIPd, LIPv, 7a, LOP, and DP). Taking into account that we sampled these areas more densely than more medial areas (i.e., IPS fundus, medial wall, and area 5), the frequency of task rule-selective neurons was still more than twice as high in the lateral areas (35%,  $n = 95$  of 274) compared with the medial areas (15%,  $n = 16$  of 104, chi-square test,  $p < 0.001$ ).

Each of the two tasks was equally well represented in the population of recorded neurons, and there was no statistically significant clustering of neurons preferring a single task within a particular area (tested by comparing proportions of neurons of each rule type per area with chi-square tests). Visual inspection of Figure 11–3 suggests a clustering of neurons selective for task A (color task rule) in monkey 2 in areas 7a, DP, LIPd, and LIPv, but this did not reach statistical significance and was not replicated in monkey 1.

Different spike rates in the two task rule conditions could reflect a difference in preparation for the upcoming task, but could also reflect a difference in the sensory features of the two cues. For example, a given neuron might be sensitive to cue color (i.e., yellow versus blue) rather than to the task rule indicated by the color of the cue. Further, differences in spike rates could combine effects of task rule and cue features. To separate these two effects, we performed an additional experiment to determine whether task rule selectivity was independent of the sensory features of the cue.

We tested an entirely new set of 192 neurons in the same two monkeys using either a color cue (yellow or blue) or a shape cue (upright or inverted triangles) to instruct the task rule (Fig. 11–1*B*). Figure 11–4 shows two examples of TASK<sup>+</sup> neurons in area 7a tested with this design. Four hundred milliseconds after cue onset, firing became markedly larger for task B trials compared with task A trials. This was true whether the task rule was conveyed by a color cue or by a shape cue. Differences in rule-selective activity developed slowly, but were maintained throughout the remainder of the delay period. In one of the two neurons (Fig. 11–1*B*, bottom), this difference persisted for more than 300 ms after the imperative stimulus appeared.

We analyzed whether neural responses during the delay period were different in the two task rule conditions. We applied a  $2 \times 2$  analysis of variance

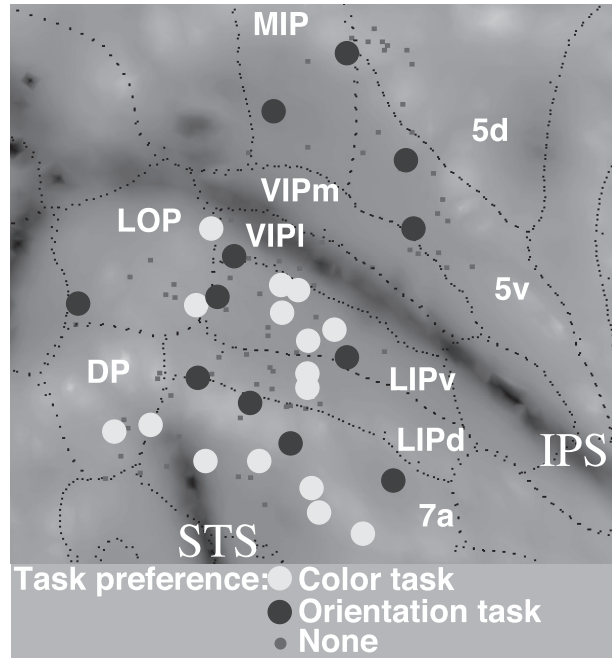


Figure 11-3 Map of flattened cortex showing the recording sites in monkey 2, derived from a magnetic resonance image that was processed using the software packages Caret and SurfFit (Van Essen et al., 2001) [retrieved in 2004 from <http://brainmap.wustl.edu/caret>]. *Broad black lines* indicate fundi of sulci. The *top* of the panel is medial and anterior; the *bottom* of the panel is lateral and posterior. *Yellow and blue dots* indicate locations of cells that fire preferentially in connection with task A or task B rules, respectively. *Small red dots* indicate recording locations of the remaining cells. Areal boundaries, although drawn as sharp lines, reflect the maximum likelihood based on a probability map and are therefore only approximate (Lewis and Van Essen, 2000).

(ANOVA) with the factors “task rule” (task A or task B) and “task instruction cue set” (colors or shapes) to each neuron’s responses during the late delay period. The results indicated that 32% of neurons (42 of 132) in the lateral wall of the IPS and the adjacent gyral surface had a main effect of task rule, which provides an independent replication of the findings based on one cue set (35% TASK<sup>+</sup> cells). Of these, two-thirds ( $n=29$ ) showed a main effect of task rule without an interaction with task instruction cue set (colors versus shapes). This indicates that most TASK<sup>+</sup> neurons reflect the task rule,

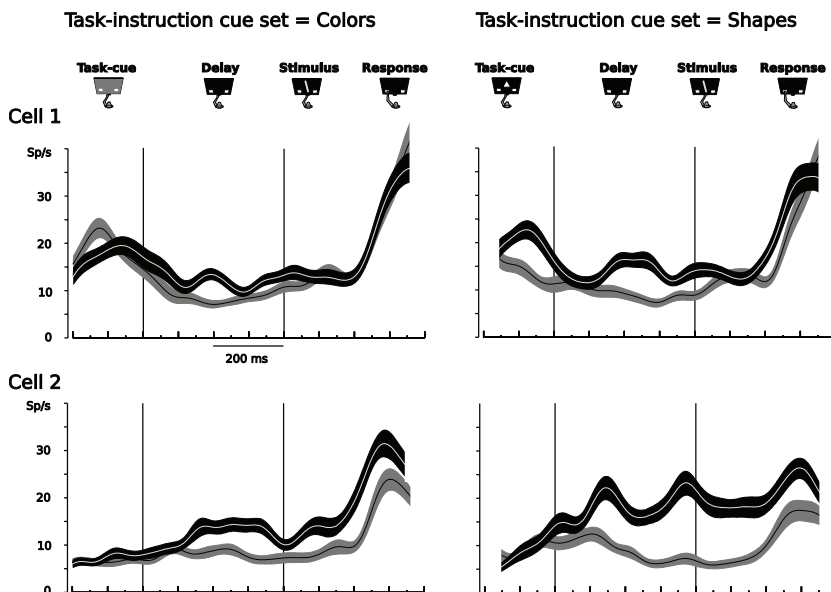


Figure 11–4 Examples of two task rule–selective cells in area 7a. *Thick black and gray traces* represent neuronal responses (mean  $\pm$  1 standard error of the mean) to color cues (*left*) and shape cues (*right*) instructing task A and task B, respectively. The *top panels* show a cell (364 trials) preferring task B. Delay activity was consistently higher for task B (for this animal, the orientation task trials), irrespective of the task instruction cue set. The *bottom panels* show a cell (384 trials) with a main effect of task (preferring task B) as well as an interaction between task and cue. The interaction is evident in the larger task-selective response in the *bottom right panel*. Sp/s, spikes per second.

independent of the way in which the rule was instructed. Outside of these regions (i.e., in the IPS fundus, medial wall, and area 5), effects were similar, albeit weaker: Only 20% of neurons showed a main effect of task rule, and in more than half of these neurons, there was an interaction between task rule and task instruction cue set.

To quantify the strength of the encoding of task rules, we examined the magnitude of the task effect using a receiver operating characteristic (ROC) analysis (Metz, 1978). This analysis measures how well an ideal observer could identify which task rule was in effect, based solely on the firing rate from a single trial. For neurons in the lateral wall of the IPS and the adjacent gyral surface, the area under the ROC curve was greater than 0.60 or less than 0.40 for 28.5% of neurons. The area under the ROC curve was greater than 0.60 or less than 0.40 for only 13.5% of neurons in more medial areas. The time course of the mean ROC area is shown for both sets of areas (Fig. 11–5; see color insert). Compared with the effect in the medial areas, task effects in the lateral

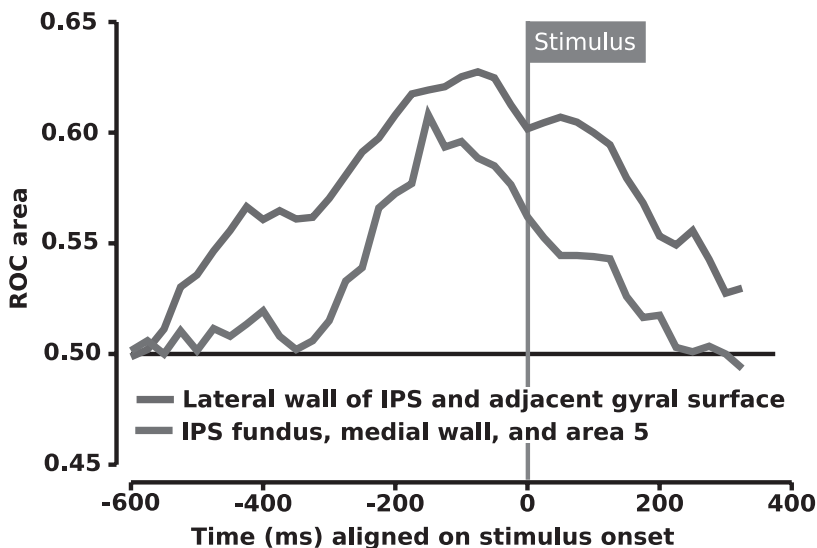


Figure 11–5 The time course of receiver operating characteristic (ROC) values for significant task cells shows that task-selective activity in the lateral intraparietal sulcus (IPS) and adjacent gyral surface (including areas LIPd, LIPv, 7a, LOP, and DP) [*red trace*] starts earlier, reaches a higher value, and is maintained for longer than task-selective activity in the IPS fundus, medial wall, and area 5 [*green trace*].

areas begin sooner, are stronger, and are sustained well after the presentation of the imperative stimulus. In contrast, the encoding of task information in the more medial areas starts later, is weaker, and is prominent only during the delay interval itself.

To determine how the presentation of the imperative stimulus affects task selectivity, we compared task selectivity immediately before and after stimulus presentation. Task encoding was very similar among neurons in the lateral bank of the IPS and adjacent gyral surface: 27% of these neurons showed a main effect of task rule in the period after the imperative stimulus compared with 29% in the late delay period. ROC analysis showed a strong correlation between task selectivity in these two intervals. Thus, these neurons continue to encode the particular task that is being performed, even after the imperative stimulus appears. This is exactly what we might expect if these neurons play a role in processing sensory information from the imperative stimulus in the context of the particular task at hand.

We have so far demonstrated that many neurons in the PPC reflect information about the task, both before and after the appearance of the imperative stimulus. In the next section, we describe the special role that  $TASK^+$  neurons play in the processing of congruent and incongruent stimuli.

## ENCODING OF CONGRUENCY

In our task-switching paradigm, incongruent stimuli are ambiguous because they are associated with different responses, depending on the task context. From the subject's perspective, only knowledge about the task can resolve the response ambiguity of incongruent stimuli. In comparison, congruent stimuli are associated with the same response alternative in both tasks. Thus, given this difference in the relevance of the task context in the congruent and incongruent conditions, the processing of congruent and incongruent stimuli is likely to differ. Imaging studies of human subjects performing task-switching and other paradigms with incongruent stimuli have concluded that stimulus incongruity leads to heightened neural activity in the PPC (Bench et al., 1993; Carter et al., 1995; Taylor et al., 1997; Peterson et al., 1999; Adelman et al., 2002), as well as in a number of frontal areas (e.g., Schlag-Rey et al., 1997; Olson and Gettner, 2002; Munoz and Everling, 2004; Nakamura et al., 2005).

In the following analyses, we first address whether neurons in the PPC show different activity after congruent versus incongruent stimuli. Then we analyze whether TASK<sup>+</sup> and task-negative (TASK<sup>-</sup>) neurons differ in their responses to congruent and incongruent stimuli.

The analyses are applied to the same neuronal data as used in the previous section. For each neuron, we determined whether spike rate reflected stimulus incongruity in the period 25–225 ms after stimulus onset. We calculated the fraction of neurons that were significantly more active after an incongruent stimulus compared with a congruent stimulus. We found that this fraction was not significantly different from chance (3.7%), and was similar to the fraction of significantly less active neurons (3.9%). At the population level, mean activity was exactly the same for incongruent and congruent stimuli ( $15.7 \pm 0.7$  spikes per second [sp/s] in both conditions). Similar results were obtained when we considered other time intervals (i.e., 50–250 ms, 100–300 ms, and 50–350 ms after onset of the imperative stimulus). Altogether, we observed neither an increase nor a decrease in firing rate after the presentation of an incongruent versus a congruent stimulus, either at the single-neuron level or at the population level, in the PPC.

Next, we tested for an effect of congruence on neuronal latency. We used a particular property of neurons in the PPC, that is, spatial tuning, to quantify neural latency. Neuronal activity in the PPC is often correlated with some spatial aspect of the task, for example, the distance of a stimulus or motor response from a particular location in space. Spatially tuned neurons are common in the PPC (Andersen et al., 1985; Colby and Goldberg, 1999; Snyder et al., 2000). Tuned spatial responses that occur around the time of a motor response may reflect the generation of a motor command (Mountcastle et al., 1975), or they may reflect an efference copy of a command that has been generated elsewhere (von Holst and Mittelstaedt, 1950). If the spatially tuned activity substantially precedes the motor output, then it may reflect a sustained sensory response

(Duhamel et al., 1992), a neural correlate of covert attentional processes (Bushnell et al., 1981), a neural correlate of motor intention (Snyder et al., 1997, 2000), or a decision variable related to the value of either a particular stimulus or a particular response (Platt and Glimcher, 1999; Sugrue et al., 2004).

There are a number of different ways in which congruency could affect the latency of a spatially tuned response component. Consider the interval that elapses between the first appearance of response-related activity in a particular brain area, and the time at which a motor response is initiated. It seems natural to think that this “neuronal-behavioral response latency” should be unaffected by factors such as congruence. However, other results are possible. For example, in the face of conflict (e.g., incongruent stimuli), the downstream mechanisms may require a higher level of certainty before a response is initiated, thereby increasing the neuronal-behavioral response latency on incongruent compared with congruent trials. As another example, when performing a sequence of effortful motor responses in which easy and difficult trials are mixed together, one might delay responses in easy trials to maintain a consistent rhythm across all trials. Most generally, neurons that show a consistent temporal relationship between activation and a particular motor response across a wide range of conditions are more likely to represent motor variables. Neurons whose temporal relationship between activation and a particular motor response depends on task condition are more likely to represent a cognitive (decision) variable. We found that parietal neurons that lacked task information ( $TASK^-$  cells) fell into the former category, whereas  $TASK^+$  cells fell into the latter category.

To perform this analysis, we considered only the subset of neurons with significant spatial tuning. We selected these neurons by comparing whether the spike rate in an interval starting 200 ms before home key release and lasting until 100 ms after home key release was significantly different for trials in which the animal moved to the right versus the left response button (Student's *t*-test, alpha level of 5%). We found that the firing rates of 62% of neurons (233 of 378) were significantly different for leftward and rightward responses.

We then determined the latency of neuronal responses in the congruent and incongruent trials. In Figure 11–6, we show an example neuron with higher firing for reaches to the left compared with the right (solid versus dashed traces). In this neuron, the divergence in firing rate occurred 41 ms sooner for congruent trials than for incongruent trials (dark gray versus light gray traces). Unfortunately, neuronal latency is difficult to measure accurately, because in these neurons (in contrast to, for example, the response of a V1 neuron to a visual transient), the change in activity is initially quite slow. As a result, small differences in instantaneous activity can lead to large differences in measured latency. In contrast, the rise time to half-maximum activity was well correlated with response latency, and was much more robust. For the example neuron, the rise time to half-maximum activity was 55 ms.

Even when using rise time to half-maximum activity, the data from individual neurons were often noisy. Therefore, we determined the neural latency



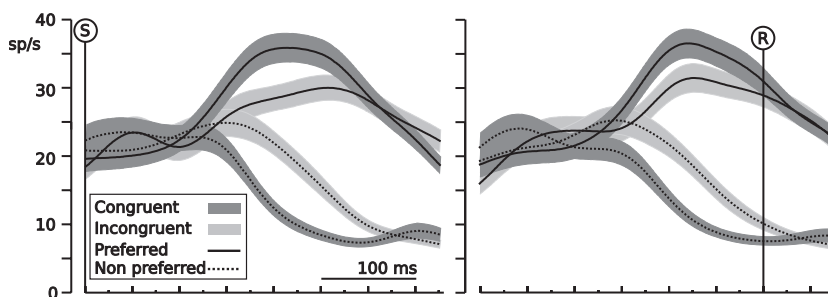


Figure 11–6 Neuron showing delayed spatial response latencies due to stimulus incongruity. Average spike rate and standard error are displayed, aligned on the onset of the imperative stimulus (S) [left], or on the onset of the response (R) [right]. The cell was spatially responsive, and fired more vigorously when the monkey reached for the left response button than for the right button. Hence, the preferred direction was to the left. The latency of this directional specificity occurs when the curves for the preferred (solid lines) and nonpreferred directions (dashed lines) diverge. Note that the divergence and the half-maximum amplitude occur earlier in the congruent condition (dark gray) than in the incongruent condition (light gray). Sp/s, spikes per second.

of the entire population of spatially tuned neurons. For each tuned neuron, we first performed a millisecond-by-millisecond subtraction of firing rate when the response was made in the preferred minus the nonpreferred direction. For example, in Figure 11–6, we subtracted the dashed lines from the corresponding solid lines. The resulting data isolate the directional component of the response. We then averaged the data across neurons and smoothed it using a low-pass filter ( $-3$  dB point of 9 Hz). This analysis (Fig. 11–7A) revealed that modulation resulting from directional preference appeared sooner in congruent trials (dark gray) than in incongruent trials (light gray). There was also a slight (19%,  $p > 0.1$ ) reduction in the maximum amplitude of direction-related activity, which came approximately 350 ms after the onset of the imperative stimulus.

The neural latencies were 90 ms in congruent trials and 113 ms in incongruent trials (Fig. 11–7A). The activity is unlikely to reflect an efference copy of the saccade command or a visual reafference response, because the neuronal activity precedes the corresponding mean saccadic latencies (202 ms and 217 ms, respectively) by more than 100 ms. The difference between congruent and incongruent neural response latencies approached, but did not reach, statistical significance ( $p < 0.08$ , Monte Carlo test). Nevertheless, this difference was highly statistically significant when a more robust measure of timing was used: Half-maximum activity was achieved 196 ms and 224 ms after stimulus onset for congruent and incongruent stimuli, respectively ( $p < 0.0003$ , Monte Carlo test). The latency differences identified by the two methods were similar (23 ms and 28 ms), although variability was substantially less for the latter measurement.

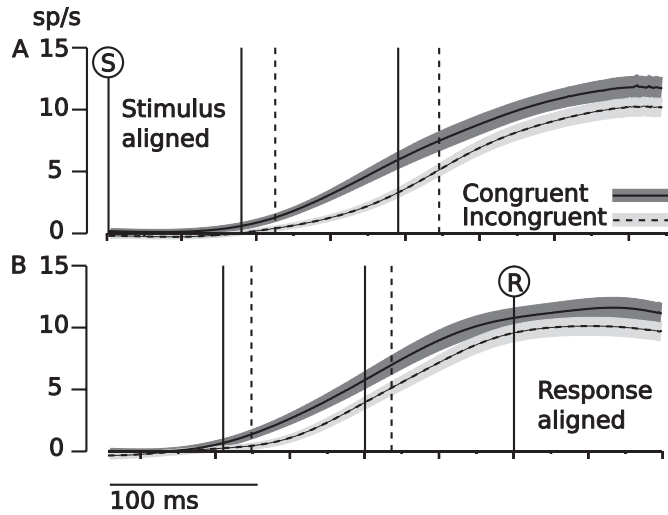


Figure 11–7 The timing of the directional response of the population of spatially tuned neurons from both animals. For each cell, the trials were sorted by the direction of the reach. Responses on null direction reaches were subtracted from responses on preferred direction reaches. The data were then averaged across cells and plotted as a function of time. The *vertical lines* indicate the onset of directional tuning and the time to half-maximum activity. *A*. Data aligned on the onset of the imperative stimulus (S). The population response to congruent stimuli starts earlier (90 ms after stimulus onset) [*left solid line*] than the response to incongruent stimuli (113 ms after stimulus onset) [*left dashed line*]. The difference in timing is similarly reflected in the time to half-maximum activity (196 ms for congruent stimuli [*right solid line*] and 224 ms for incongruent stimuli [*right dashed line*]). *B*. Data aligned on the onset of the arm response (R). The population response to congruent stimuli starts earlier (197 ms before response onset) [*left solid line*] than the response to incongruent stimuli (178 ms before response onset) [*left dashed line*]; henceforth, onset before the alignment point will be indicated by a minus sign. The difference in timing is similarly reflected in the time to half-maximum activity (–101 ms for congruent stimuli [*right solid line*] and –83 ms for incongruent stimuli [*right dashed line*]). Sp/s, spikes per second.

We used two different alignments. First, we aligned individual trials on the onset of the imperative stimulus, emphasizing differences in the perceptual and cognitive components of processing (Fig. 11–7A). Next, we aligned on the onset of the button release, emphasizing differences in cognitive and motor components of processing (Fig. 11–7B). Even when aligned on the response onset, both the divergence time and half-maximum time occurred sooner in

the congruent compared with the incongruent condition (by 19 ms,  $p < 0.08$ ; by 18 ms,  $p < 0.001$ , respectively).

To examine this result further, and to explore the possibility that neurons that maintain task information may play a different role in stimulus-response mapping than neurons that do not maintain task information, we analyzed neurons with and without task information separately (TASK<sup>+</sup> and TASK<sup>-</sup> neurons).

We repeated the same analysis that we performed on the population of all spatially tuned neurons on the separate subpopulations of TASK<sup>+</sup> and TASK<sup>-</sup> neurons. Effects in neurons preferring task A ( $n = 37$ ) and task B ( $n = 40$ ) were similar, and therefore these two subpopulations of neurons were pooled.

We expected that, in a neuron population representing a motor variable (including an efference copy signal), the neuronal congruency effect would match the behavioral congruency effect. We found that this was true for TASK<sup>-</sup> cells, but not for TASK<sup>+</sup> cells. Incongruent stimuli resulted in a 15-ms slowing of the time to the half-maximum neuronal response in TASK<sup>-</sup> neurons (Fig. 11-8A) [215 ms versus 230 ms] and a 49-ms slowing in TASK<sup>+</sup> neurons (Fig. 11-8C) [164 ms versus 213 ms]. Although these congruency costs were statistically significant in both neuronal populations ( $p < 0.007$  and  $p < 0.0004$ , respectively, Monte Carlo test), only the effect in the TASK<sup>-</sup> cells matched the behavioral (arm movement) effect (10–16 ms).

The marked difference in the timing of TASK<sup>-</sup> and TASK<sup>+</sup> neuronal responses can be better appreciated when the data are aligned to the time of the motor response (arm movement). With this alignment (Fig. 11-8B), it can be seen that TASK<sup>-</sup> cell activity was time-locked to the arm movement, with the time to half-maximum response differing by only 5 ms in congruent compared with incongruent trials. In contrast, TASK<sup>+</sup> cell activity was independent of the motor response, with a 32-ms difference in time to half-maximum activity in congruent compared with incongruent trials (Fig. 11-8D) [ $p < 0.01$ , Monte Carlo test].

Thus, the activity of TASK<sup>-</sup> cells, but not TASK<sup>+</sup> cells, appears to reflect a motor variable. However, animals moved not only their arms to the response button, but also their eyes. Might the activity of TASK<sup>-</sup> cells reflect arm movement responses and the activity of TASK<sup>+</sup> cells reflect eye movement responses? We were able to rule out this intriguing possibility. Eye movements were typically initiated approximately 150 ms before the arm movement. However, these eye movement responses were time-locked to the arm movement responses. Relative to the onset of the arm movement, mean saccade latencies differed by no more than 3 ms (black and gray arrows in Figs. 11-8B and 11-8D). Therefore, the timing of TASK<sup>+</sup> neurons cannot be explained by the timing of either saccades or arm movements.

These results clearly dissociate the activity of TASK<sup>+</sup> neurons from both sensory variables (Fig. 11-8C) and motor variables (Fig. 11-8D). These dissociations indicate that an independently defined subset of parietal neurons “solves” the stimulus-response mapping problem sooner in congruent

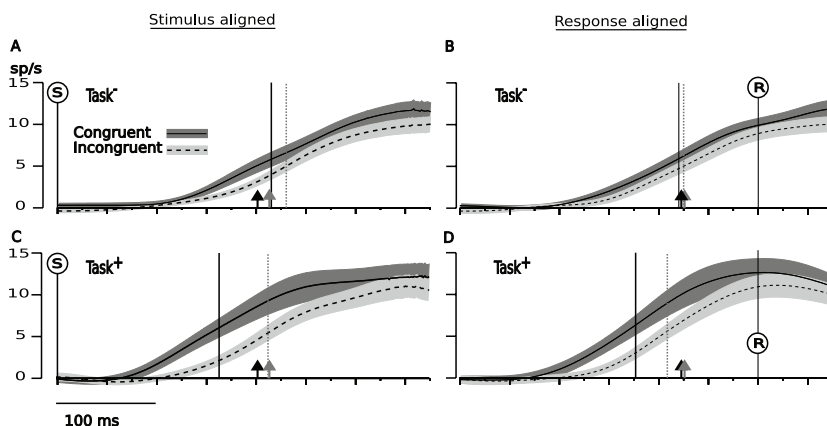


Figure 11-8 Onset of neural directional response (preferred minus nonpreferred direction) as a function of task selectivity and imperative stimulus congruency (spatially tuned neurons only). *A*. The difference in the time to half-maximum activity for congruent trials (215 ms) [solid vertical line] and incongruent trials (230 ms) [dashed vertical line] is similar to the behavioral response latency difference. *B*. Same data as in *A*, but aligned on the arm response onset. The latency difference between congruent (−80 ms) and incongruent (−75 ms) is 5 ms. The eyes began to move to the target approximately 150 ms before the arm began to move. The average saccade response times are indicated by black (congruent) and gray (incongruent) arrows. *C*. Similar to *A*, but for the task-positive ( $\text{Task}^+$ ) cells. In contrast to the task-negative ( $\text{Task}^-$ ) cells, there is a large latency difference in the time to half-maximum activity between congruent (164 ms) and incongruent trials (213 ms). *D*. Similar to *B*, but for the  $\text{TASK}^+$  cells. The latency difference between congruent (−123 ms) and incongruent (−91 ms) trial is 32 ms. S, stimulus; R, response.

compared with incongruent trials, even when the data are aligned on the motor response.

In summary, analyses of the effects of congruency suggest that  $\text{TASK}^+$  neurons play a substantially different role than  $\text{TASK}^-$  neurons in sensory-to-motor transformations.  $\text{TASK}^-$  neurons in the PPC appear to reflect motor variables.  $\text{TASK}^+$  cells, unlike  $\text{TASK}^-$  cells, are influenced by task context, and the observation that  $\text{TASK}^+$  cells respond so differently from  $\text{TASK}^-$  cells, unless, under incongruent compared with congruent conditions (Fig. 11-8*B* versus 11-8*D*), supports the idea that  $\text{TASK}^+$  cells do not merely reflect sensory or motor variables, but instead are involved in applying task rules during sensorimotor processing.

## GENERAL DISCUSSION

We studied rule representation and rule-based processing of stimuli in monkeys using a task-switching paradigm. The animals were able to interleave

two tasks quite well, with speed and accuracy comparable to those of human subjects. Surprisingly, however, the monkeys did not show switch costs, which are a hallmark of human performance in these types of paradigms. We went on to record data from neurons in the PPC to study the neural mechanisms underlying task-switching and rule representation in the monkey. Our most important findings from these recordings are that parietal neurons encode information about abstract task rules, and play a role in disambiguating response-ambiguous stimuli.

### Comparison of Human and Monkey Behavior

Overall, task-switching performance is similar in monkeys and humans, although monkeys are somewhat faster than humans (Fig. 11–2). We do not take the faster RTs in monkeys versus humans as evidence of superior behavioral performance. For example, physical differences in the conduction pathways of the smaller brain (Ringo and Doty, 1994) or mechanical factors in the musculature could partially explain the differences in speed.

Monkeys show no difficulty in switching their attention from one task to another (little or no residual switch costs) [Fig. 11–2]. However, their ability to focus on the task at hand is comparatively poor: Their performance is significantly affected by irrelevant stimulus features (high incongruency costs). The opposite is true for humans, who have difficulty switching, but little difficulty maintaining attention on the appropriate stimulus features.

We considered the possibility that monkeys, unlike humans, memorized all separate cue-target-response combinations, and then used a memory-based strategy. The use of a memory-based strategy might explain the absence of switch costs, because in this case, the animals would not actually be switching between two different rules. Two pieces of evidence refute this idea: (1) We found small switch costs when ITIs were very short, suggesting that monkeys treat the two tasks differently. (2) An animal successfully responded to 11 completely novel stimuli, which would not be possible if it used a memory-based strategy.

It is also possible that the varying amounts of practice might explain the difference in human and monkey switch costs. The humans in our study performed only 3000 trials, whereas monkeys performed tens or hundreds of thousands of trials. However, a recent study from our laboratory demonstrates that switch costs are retained in humans after more than 30,000 practice trials (Stoet and Snyder, in press).

The existence of persistent switch costs and lower incongruency costs in humans compared with monkeys could be two manifestations of a single process. Humans appear to be able to “lock in” a particular task, thereby minimizing incongruency costs, but paying the price of having to take time to “unlock” the mapping when the task switches. We experience this “unlocking” as a persistent switch cost. In comparison, monkeys cannot lock in a particular task and therefore are distracted by irrelevant stimulus dimensions, resulting

in incongruency costs. However, because they do not lock in a task in the same way a human does, they do not experience persistent switch costs.

Both humans and monkeys show nonpersistent switch costs, that is, costs that appear only with short preparation times. Nonpersistent 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 incongruency nor incurs persistent switch costs.

A general theory of task-switching should offer an explanation for species-specific effects. It seems unlikely that humans suffer from an undesirable cost in task-switching that monkeys completely avoid. We hypothesize that human switch costs reflect an evolutionarily advantageous cognitive mechanism that helps to maintain focused attention on a particular task for long periods.

Of course, as in many comparative studies, we cannot rule out the possibility that our results were influenced by some minor difference in procedures. 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).

The finding that monkeys do not show persistent switch costs is interesting, but also somewhat disappointing, because this absence means that monkeys cannot be used to investigate the neural basis of persistent switch costs in humans. 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 (because monkeys, like humans, can learn to switch between tasks quite well); a good model for the ability to prepare tasks in advance; a good model for task incongruency; a good model for nonpersistent switch costs; and a good model for looking at task representations.

### **Representation and Application of Rules in the Monkey Posterior Cortex**

We have presented evidence that a subset of neurons (TASK<sup>+</sup>) in the PPC, concentrated in the lateral bank of the IPS and on the adjacent angular gyrus, responds selectively to cues for different task rules.

The encoding of information about task rules is often called “cognitive set.” We propose that true cognitive set signals should exist completely independent of sensory signals. This definition distinguishes true cognitive set signals, such as those reported in the prefrontal and premotor cortices (Konishi et al., 2002; Nakahara et al., 2002; Wallis and Miller, 2003) from signals that reflect sensory information, but are modulated by nonsensory variables (e.g., spatial attention or other task contingencies) [Britten et al., 1996; Treue and Maunsell,

1996; Snyder et al., 1997; Colby and Goldberg, 1999; Bisley and Goldberg, 2003].

Until recently, it appeared that task-related signals in the parietal cortex fell into the latter category and not the former, encoding task-relevant sensory information, not abstract signals related to task preparation (Assad, 2003). The current results from the parietal cortex, in contrast, clearly demonstrate the encoding of task-rule information in advance of receiving stimulus information. The task-switching paradigm separates out the presentation of the instruction of which rule is to be used from the presentation of the stimulus to which that rule is to be applied. This separation is extremely useful, allowing us not only to identify those cells involved in task coding (TASK<sup>+</sup> cells), but also to study sensorimotor processing in these cells.

To study the effect of task-rule information on stimulus processing, we compared trials using congruent stimuli (stimuli that require the same response in the two tasks) with trials using incongruent stimuli (stimuli that require different responses in the two tasks).

This comparison allows for a simple test of neural responses to incongruency, and has been explored in human imaging studies. Brain imaging studies of the human PPC reveal an increased blood-oxygen level–dependent signal after incongruent stimuli (Bench et al., 1993; Carter et al., 1995; Taylor et al., 1997; Peterson et al., 1999; Adelman et al., 2002). We did not observe increased neural activity in our population of recorded neurons. There are many reasons why the results from functional magnetic resonance imaging (fMRI) and neurophysiology experiments might differ. First, the human studies used a linguistic task (Stroop task), whereas our study used a nonverbal task. It is possible, for example, that the involvement of the parietal cortex in conflict depends on the type of task (e.g., verbal versus nonverbal). Second, the PPC may be used differently in humans and monkeys. Given that the human PPC is larger and more developed in humans, it is likely that the human PPC fulfills many functions not available to monkeys. Finally, unit recording and fMRI results may not be directly comparable. For example, Logothetis et al. (2001) simultaneously recorded blood-oxygen level–dependent signals and microelectrode recordings, and concluded that fMRI reflects input and intracortical processing rather than spiking output.

We found a surprising result when comparing neuronal response during congruent and incongruent trials. Because incongruent stimuli are associated with longer behavioral RTs than congruent stimuli, it was not surprising to find that incongruent stimuli were also associated with longer neuronal latencies. In TASK<sup>-</sup> cells, incongruity had similar effects on behavioral and neuronal latency differences (15 ms and 10–16 ms, respectively). This can be seen graphically by the fact that, when aligned on response onset, the neuronal responses of TASK<sup>-</sup> cells are indistinguishable (Fig. 11–8B). In contrast, TASK<sup>+</sup> cells showed a neuronal effect of incongruity that was much larger than the behavioral effect (49 ms versus 10–16 ms, respectively): TASK<sup>+</sup> cell responses

do not overlap one another when aligned on the time of the motor response (Fig. 11–8D). Furthermore, by comparing the upper and lower halves of Figure 11–8, it can be appreciated that  $TASK^+$  cells encode the animal's upcoming choice of where to move sooner than  $TASK^-$  cells, especially in congruent trials.

These results have important implications. The finding that  $TASK^+$  neurons encode the animal's choice of where to move substantially sooner than  $TASK^-$  neurons supports the idea that  $TASK^+$  neurons play an important role in the task-switching paradigm, and that this role is distinct from that played by  $TASK^-$  neurons (Stoet and Snyder, 2004).  $TASK^+$  cells are likely to help map sensory stimuli onto motor responses, given a particular task context, whereas  $TASK^-$  cells represent the outcome of the mapping. Our results dissociate  $TASK^+$  cell responses from both sensory inputs and motor outputs. This suggests that  $TASK^+$  cells play an intermediate role, helping to map sensory stimuli onto motor responses. In contrast,  $TASK^-$  cell responses are well correlated with the motor response. This suggests that  $TASK^-$  cells represent the outcome of the sensory-to-motor mapping. This interpretation is consistent with the idea that  $TASK^-$  cells carry either a motor command signal (Mountcastle et al., 1975) or an efference copy signal (von Holst and Mittelstaedt, 1950).

Furthermore, by isolating the responses of  $TASK^+$  and  $TASK^-$  cell populations, we are able to see that monkeys do not always respond as soon as parietal neurons encode a decision. Based on the neuronal recording, we would have expected that responses in the congruent trials would be approximately 50 ms faster than in incongruent trials, but that is not what we observed. Instead, button presses in difficult (congruent) trials are delayed relative to button presses in easy (congruent) trials. What could explain the finding that  $TASK^+$  cells encode the correct response in congruent trials nearly 50 ms sooner than in incongruent trials, and yet the behavioral cost of stimulus incongruity is only 10–16 ms? Put differently, why don't monkeys respond still faster to congruent stimuli, given that their parietal cortices encode the correct response so quickly? The parietal cortex may not be the only brain area that performs this sensory-to-motor computation. It is possible that parallel pathways are involved, with different latencies in the different pathways in congruent and incongruent trials. In the absence of conflict (congruent trials),  $TASK^+$  cells in the parietal cortex may compute an answer first. However, in the presence of conflict (incongruent trials), it may be that another area (e.g., the frontal cortex) computes a response more quickly than the parietal cortex. As a result, behavioral RTs would be determined by  $TASK^+$  cell latencies in congruent trials, but not in incongruent trials.

### The Role of Language

The implications of this study go beyond understanding task-specific processing in simple cognitive tasks. Rule representation and rule-dependent stimulus processing is a hallmark of human cognition, and characterizing the



neural underpinnings of a nonverbal task-switching paradigm may help us to approach the more complex context-dependent processing that occurs in human cognition. Like the incongruent stimuli of the current study, particular words and phrases have multiple possible meanings that are disambiguated by context. For example, the meaning of a linguistic expression depends on the meaning of the words that immediately precede or follow it (Gerrig and Murphy, 1992; Strohner and Stoet, 1999). It is intriguing to try to identify the origins of human language skills in the abilities of present-day nonhuman primates (Gardner and Gardner, 1969; Premack, 1971; Ujhelyi, 1996), and to determine whether these origins might involve the PPC and its role in context-specific processing (Gurd et al., 2002). This is a very important question, albeit far from being answered. A more fundamental question is whether human language skills can help us to understand basic differences in understanding human and animal rule-guided behavior.

Humans can learn a new rule in seconds, simply by following verbal instructions, and this constitutes a fascinating and fundamental difference between humans and monkeys. Arguably, it is the nature of language that makes efficient representation and quick communication possible, and language is unique in doing so. Any attempt to communicate a rule other than with words either would not be as efficient or would involve some of the symbolic characteristics unique to language. Therefore, it is not too far-fetched to assume that language is a key component in understanding the differences between human and animal rule-based behavior and cognition. Unfortunately, very little is known about the role of language in explaining differences between human and animal rule use. We would like to mention three of the most important questions that must be answered to improve our understanding of this issue.

First, there is the question of how the process of acquisition of verbal and nonverbal rules differs in humans. It is possible, for example, that humans process nonverbal rules by first conceptualizing them in a verbal format. Given that humans are able to act on rules before they are able to express them verbally, however, this seems unlikely (Bechara et al., 1997). Conversely, verbal rules might first be converted into a nonverbal currency before they can actually be applied in a task. Finally, verbal and nonverbal rules may be handled in completely different ways in the human.

Closely related to the issue of rule acquisition and application is the issue of rule representation. Does language play a role in rule representation only as a tool during the acquisition of the rule, or is language an essential component of the representation itself? It is possible that representations of rules differ depending on how they are acquired; one can imagine that identical rules, conveyed directly through language or learned through some nonverbal mechanism (e.g., trial-and-error, imitation), might be represented in different parts of the brain.

Finally, does the lack of verbal language skills in monkeys imply that they represent rules differently? The answer may depend on the particular rule—on

its complexity, for example—or on its amenity to being expressed by language. The null hypothesis is that simple rules are represented and implemented similarly in the two species. However, introspection suggests that language is incredibly important to human cognition, whereas monkeys show no evidence of any similar abilities. Furthermore, human cortices are functionally lateralized, and this lateralization appears to be related, at least in part, to verbal abilities. This suggests that verbal abilities have had a large effect on our cortical architecture. It is intriguing to consider that human language abilities may relate to the ability, which monkeys lack, to lock in to a particular task.

We believe that monkeys provide an essential model system, if not for directly understanding human cognition, then at least for developing the tools and hypotheses needed to approach the issue in humans. We believe that the current findings demonstrate that task-switching paradigms provide an excellent entry point for this work.

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