Correlates of Stimulus–Response Congruence in the Posterior Parietal Cortex

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Abstract

■ Primate behavior is flexible: The response to a stimulus often depends on the task in which it occurs. Here we study how single neurons in the posterior parietal cortex (PPC) respond to stimuli which are associated with different responses in different tasks. Two rhesus monkeys performed a task-switching paradigm. Each trial started with a task cue instructing which of two tasks to perform, followed by a stimulus requiring a left or right button press. For half the stimuli, the associated responses were different in the two tasks, meaning that the task context was necessary to disambiguate the incongruent stimuli. The other half of stimuli required the same response irrespective of task context (congruent). Using this paradigm, we previously showed that behavioral responses to incongruent stimuli are significantly slower than to congruent stimuli. We now demonstrate a neural correlate in the PPC of the additional processing time required for incongruent stimuli. Furthermore, we previously found that 29% of parietal neurons encode the task being performed (task-selective cells). We now report differences in neuronal timing related to congruency in task-selective versus task nonselective cells. These differences in timing suggest that the activity in task nonselective cells reflects a motor command, whereas activity in task-selective cells reflects a decision process. ■

INTRODUCTION

Human responses to stimuli depend on the task being performed. When the task changes, a stimulus that was previously task-relevant may become task-irrelevant. Task-irrelevant stimuli may, nonetheless, interfere with task performance. The phenomenon of how changes in task instructions affect behavior and neural activity, and of how irrelevant stimuli may interfere with task performance, has been studied using a variety of experimental paradigms, including the Stroop task (MacLeod, 1991; Stroop, 1935), the flanker task (Eriksen & Eriksen, 1974), the saccade/antisaccade task and variants (Munoz & Everling, 2004; Fischer & Weber, 1992), the countermanding task (Logan & Cowan, 1984), spatial-compatibility tasks (Nakamura, Roesch, & Olson, 2005; Olson & Gettner, 2002), task-switching paradigms (Stoet & Snyder, 2003a; Jersild, 1927), and other task designs (Toth & Assad, 2002).

A common feature of these paradigms is that a single stimulus may be associated with two or more different responses, depending on the task conditions. For example, in a Stroop task, subjects are required to name the ink color of a word that is printed in an incompatible color (e.g., ''red'' printed in green ink). We refer to such stimuli as ''response incongruent'' or simply ''incongruent.'' In contrast, a ''congruent'' stimulus is associated with just a single response (e.g., in a Stroop task the word ''red'' printed in red). Behavioral responses to incongruent stimuli are slower and less accurate than responses to congruent stimuli. This difference in response latencies is likely to reflect additional processing needed to resolve a stimulus–response mapping conflict, and has been observed in both humans and monkeys (Stoet & Snyder, 2003a). In humans, the posterior parietal cortex (PPC) appears to be critically involved in the processing of incongruent stimuli (Adleman et al., 2002; Peterson et al., 1999; Taylor, Kornblum, Lauber, Minoshima, & Koeppe, 1997; Carter, Mintun, & Cohen, 1995; Bench et al., 1993). In a Stroop task, for example, blood oxygenation level-dependent (BOLD) signals increase in the PPC in response to an incongruent compared to a congruent stimulus. However, stimulus–response conflict is more typically associated with frontal activations (Nakamura et al., 2005; Badre & Wagner, 2004; Botvinick, Cohen, & Carter, 2004; Kerns et al., 2004; Langenecker, Nielson, & Rao, 2004; Munoz & Everling, 2004; Weissman, Giesbrecht, Song, Mangun, & Woldorff, 2003; Mead et al., 2002; Olson & Gettner, 2002; van Veen & Carter, 2002; Zysset, Muller, Lohmann, & von Cramon, 2001; Everling & Munoz, 2000; Leung, Skudlarski, Gatenby, Peterson, & Gore, 2000; Peterson et al., 1999; Schlag-Rey, Amador, Sanchez, & Schlag, 1997; Larrue, Celsis, Bes, & Marc-Vergnes, 1994; Bench et al., 1993; Pardo, Pardo, Janer, & Raichle, 1990).

In the current study, we use monkeys to study the processing of incongruent stimuli. Instead of the commonly used Stroop paradigm, we employ a task-switching paradigm. We have extensively reported on the behavior

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and the neural correlates of behavior in this paradigm (Stoet & Snyder, 2003a, 2003b, 2004, 2006). Trials of two tasks were randomly interleaved (Figure 1A). Each trial started with the presentation of a task cue, followed by a delay period. The task cue informed the monkey whether to perform the color or the orientation task (see below) on the upcoming imperative stimulus. For each task, we used two different task cues, such that we could determine whether neurons responded to the cue itself, to the information that the cue conveyed regarding the task, or to both.

Each imperative stimulus had two critical features, color and shape, but only one was relevant in each task. In the color task, monkeys categorized the color of the stimuli as red or green, whereas in the orientation task, the animals categorized the line orientation as vertical or horizontal. Each stimulus required either a left or right button press. Monkeys reached from a paw resting position to one of the two continuously displayed squares on the screen to indicate the response (see Methods for details). It is important to note in this study that imperative stimuli were either congruent or incongruent. Congruent stimuli would require the same response in both tasks. For example, a red vertical line would require the monkey to press the left button in both tasks because ''red'' requires a left response in the color task and ''vertical'' requires a left response in the orientation task (see Figure 1A for stimulus–response associations). Incongruent stimuli would require opposite responses in the two tasks. For example, a red horizontal line would require the monkey to press the left button in the color task (red = left), but the right button in the orientation task (horizontal = right).

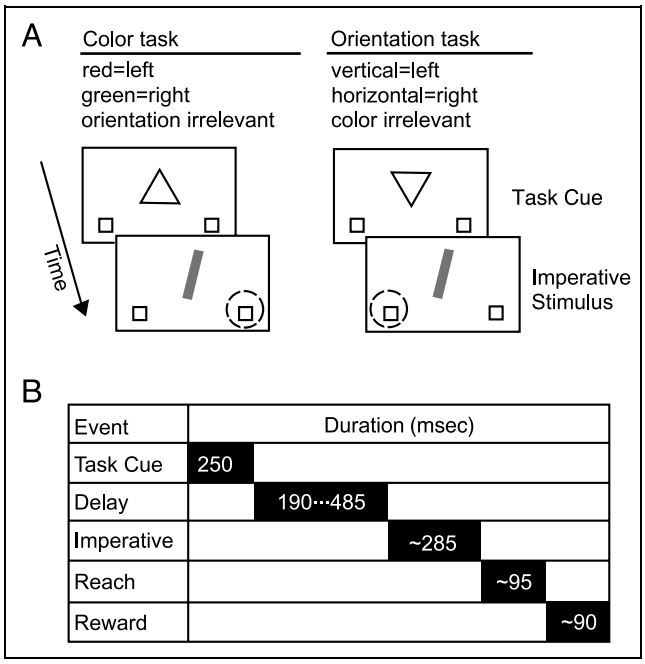

Figure 1. Illustration of the paradigm. (A) Trials of two tasks were interleaved. In the color task, monkeys were trained to respond to the color of the imperative stimulus. In the orientation task, they were trained to respond to the orientation of the stimulus. Two small white squares on the left and right of the screen were continuously displayed over a black background to indicate the two alternative reach end points (response buttons). Each trial started with a task cue (display time 250 msec). In the color task, the task cue was a regular white triangle (or a yellow screen) on the black background. In the orientation task, the task cue was a 180° rotated triangle (or a blue screen). The task cue was followed by a delay period (190–485 msec), which was then followed by presentation of the imperative stimulus. Imperative stimuli were either red or green horizontally or vertically oriented lines. From trial to trial, there was a slight random variation in color shading and orientation (see Methods for rationale). Incongruent imperative stimuli (e.g., a green vertical line) required different responses in the two tasks (e.g., a right response in the color task, but a left response in the orientation task, as illustrated with the dashed circles around the right or left response buttons). Congruent stimuli required identical responses in the two tasks. (B) Overview of the timing of events.

We previously reported that nearly one third of the cells in the PPC encode which of the two tasks the monkey is preparing to perform (Stoet & Snyder, 2004). In the current study, we reanalyzed the same data from that study in order to address a completely different issue. We ask whether individual parietal neurons reflect differences in stimulus congruence, either in the magnitude or in the timing of their activity. In contrast to the human BOLD results previously cited, we find essentially no difference in the magnitude of responses to congruent versus incongruent stimuli. We do, however, find a difference in neuronal latency. Although behavioral responses to congruent and incongruent stimuli in the monkey differ by 10–16 msec, neuronal responses differ by nearly twice as much.

We hypothesized that task-selective ($TASK^+$) cells, as identified by Stoet and Snyder (2004), would more likely be involved in selecting a particular motor response than task nonselective ($TASK^-$) cells, as performing the correct sensory to motor transformation requires not just stimulus information but also a representation of the current task. We therefore split the data into $TASK^+$ and $TASK^-$ cells. We find that the effect of congruence on $TASK^-$ cell latency is similar to the behavioral effect, consistent with a representation of the motor command. The effect of congruence on $TASK^+$ cell latency is much larger, however. This unexpected result indicates that monkeys do not always respond as soon as the sensory–motor transformation has been computed, and implicates $TASK^+$ parietal neurons in this transformation process.

METHODS

Two adult rhesus monkeys (*Macaca mulatta*) performed a task-switching paradigm. Animals were seated in a sound-attenuating dark room facing a touch sensitive screen (30 × 20 cm) at a distance of 25 cm. Animals performed between 1500 and 3000 trials per experimental session.

A capacitive home key (Efector, Exton, Pennsylvania) was positioned 2 cm below the screen, and animals used this as a resting position for their left paw. Trials would not start unless their paw touched this key. Each trial began with a visual task cue that prompted one of the two tasks, which were performed in randomly interleaved order (Figure 1). Task cues were presented by setting the screen color to yellow or blue, or by displaying an upright or inverted white equilateral triangle (14.7°) at screen center for 250 msec (Figure 1). A yellow screen had the same meaning as an upright triangle and a blue screen had the same meaning as an inverted triangle. The advantage of using two distinct types of task cues is discussed elsewhere (Stoet & Snyder, 2004) and is irrelevant for the purposes of the current study.

The task cue was followed by a delay (190–485 msec, Figure 1B). The delay was held constant within a session, and for the majority of sessions this delay was over 400 msec. The task cue was followed by a centrally positioned imperative stimulus. This stimulus instructed a paw movement from the home key to one of two white squares, positioned 16° to the left or right of the screen center. The two white squares in the bottom left and right corners of a touch-sensitive screen functioned as response buttons and were visible throughout the entire trial.

The imperative stimulus disappeared at response initiation (paw lift-off from the home key). This disappearance encouraged the monkey to evaluate the stimulus and make a choice to press the left or right button before lifting its paw from the home key. In the color task, monkeys based their decision to move to the left or right on the color of the upcoming stimulus. In the orientation task, monkeys based their decision on the vertical or horizontal orientation of the upcoming stimulus. Each stimulus was both colored and oriented horizontally or vertically, but only one stimulus dimension was relevant in each trial. Half of the stimuli were incongruent, that is, associated with different response buttons in the two tasks, and the other half were congruent, that is, associated with the same response button in the two tasks.

Imperative stimuli were colored bars (6.9° × 0.7°) oriented within 10° of either horizontal or vertical, located at a random location within 5° of screen center. Bar color was randomly chosen from many shades of red and green. The many combinations of colors and orientations were intended to encourage the use of general rules rather than a ''lookup table'' strategy for solving the tasks (see Stoet & Snyder, 2003a, 2004 for further details), including slight differences in the stimuli and tasks for the two animals (see Stoet & Snyder, 2003b for behavioral evidence that the animals in our studies prepared tasks on cue presentation, in advance of the appearance of the imperative stimulus).

Before data collection started, animals were well trained and behavioral performance was similar in the two animals. During task performance, we measured behavior and the spike rate of single neurons in the PPC. Behavioral measures included reaction time (RT; the time between stimulus onset and home key release), movement time (MT; the duration of the arm movement), saccade reaction time (SRT; the time between stimulus onset and the start of the saccade toward the correct response button, measured using a scleral search coil in about 2/3 of sessions; eye movements were not restricted), and the percentage of response errors (PE).

We recorded the activity of single neurons from the two animals using tungsten microelectrodes (FHC, Bowdoinham, ME) inserted through a grid with 1-mm spacing (Crist Instrument, Hagerstown, MD). Recording chambers were attached flush to the skull at 8 mm P, 12 mm L (Horsley-Clarke coordinates). Datasets, consisting of an average of 250 trials, were recorded from all isolated neurons. Off-line analyses matching recording depth and grid position with data from a brain image indicated that we recorded in and around the intraparietal sulcus (IPS), including areas LIPd, LIPv, 7a, LOP, and DP, IPS fundus, medial wall, and area 5 (see Stoet & Snyder, 2004 for a complete reconstruction of recording site locations).

Only data from correct trials were analyzed. Because monkeys made relatively few errors and because we could not reliably distinguish between errors that were due to motivational or cognitive difficulties, we did not analyze error trials in detail.

We assayed for task selectivity by testing the difference in mean spike rate between the two task conditions (Stoet & Snyder, 2004). For data collected using one cue type (yellow or blue screen, upright or inverted triangle), neurons showing a significant difference in firing rate in the 150 or 250 msec (depending on the delay interval used during recording) before stimulus onset were classified as task-selective ($TASK^+$) cells (Student's t test, alpha level of 5%). For neural data collected with both cue types, $TASK^+$ cells were defined as having a significant main effect of task in a two-way analysis of variance with factors task rule (color and orientation task) and cue type (yellow or blue screen, upright or inverted triangle) in the 250-msec delay before stimulus onset. All cells not classified as $TASK^+$ cells were defined as $TASK^-$ cells. Most of the $TASK^+$ neurons were found in the lateral bank of the IPS and on the adjacent gyral surface, including areas LIPd, LIPv, 7a, LOP, and DP. Taking into account the fact that these areas were more densely sampled than more medial areas (i.e., the IPS fundus, medial wall, and area 5), the frequency of $TASK^+$ was more than twice as high in the lateral areas (35%, $n = 95$ out of 274) compared to the medial areas (15%, $n = 16$ out of 104, χ^2 test, $p < .001$).

A neuron was defined as directionally selective if it had a significant difference in firing rate in the 300-msec period starting 200 msec before response onset (Student's

t test, alpha level of 5%). We determined the time of onset of directional selectivity relative to stimulus onset by first separating trials into rightward and leftward responses, and then calculating mean firing rates as a function of time in 1-msec bins. Data were then low-pass-filtered (−3 dB point of 9 Hz, the equivalent of convolving with a Gaussian of *SD* ~14 msec). The *onset of directional selectivity* was defined as the start of the first 100-msec interval in which firing rate for the two response directions differed by at least two standard errors in each consecutive 1-msec bin.

In order to compare neural data in congruent and incongruent conditions, 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. Next, we aligned on the onset of the button release, emphasizing differences in cognitive and motor components of processing.

We used two different measures for expressing the neural latency of directional selectivity. The first measurement, described above, is very susceptible to noise. This is because the rate of change is very low at the start of the movement, so a small amount of noise results in a large difference in latency. The second measurement is the time to half the maximum difference in activity. In contrast to the first measure, the half-maximum measure is made at a time when the rate of change is quite high, and therefore, the actual value is much less influenced by noise.

We performed Monte Carlo analyses to establish the significance of neural spatial-response latencies and half-maximum times. In each Monte Carlo analysis, we repeated our analysis for determining spatial-response latency and half-maximum time 3000 times after randomly assigning each trial as congruent or incongruent (as for the data shown in Figures 3 and 4), or randomly assigning a cell to the $TASK^+$ or the $TASK^-$ population (Figure 4). We then used the distribution of results from the shuffled data to determine the probability of obtaining our actual response (unshuffled data) by chance.

Data analyses were performed with custom software and the statistical package R (R Development Core Team, 2005).

RESULTS

Behavior

Data were recorded in 87 sessions, for 52,111 trials in Monkey 1 (M1) and 44,310 trials in Monkey 2 (M2). No data were discarded. Behavioral performance was similar in the two monkeys. RT was 284 ± 37 msec (M1) and 284 ± 49 msec (M2), respectively. Success rates were 95.3% (M1) and 91.5% (M2). Mean MT was 96 ± 52 msec in M1 and 98 ± 31 msec in M2. The average time needed to complete the response (RT + MT) was 380 (M1) and 382 (M2) msec. Monkeys typically made a saccade from the imperative stimulus to the response button of choice; the mean SRT was 192 ± 32 (M1) and 223 ± 54 (M2) msec.

In order to study how stimulus congruence affects sensory–motor processing, we first tested whether congruency affects the speed and accuracy of behavioral performance. For each animal, we compared RT, MT, and SRT in congruent and incongruent conditions across all sessions with Student's *t* tests, and compared error rates with χ^2 tests (Table 1). Incongruity slowed RT by 10 msec in M1 and by 16 msec in M2; MT was slowed by 18 and 19 msec, respectively; SRT was slowed by 11 and 10 msec, respectively. For each measurement (RT, MT, and SRT) and in each of the two animals, the pooled standard error was less than 1 msec. PE was increased by 7.4 and 12.6 percentage points. All tests reached statistical significance ($p < .001$) for both animals. In summary, behavioral performance was slower and less accurate in incongruent than in congruent trials.

Neural Response

Next, we tested the effects of congruency on neural activity. We recorded from 378 isolated neurons in the right PPC of the two animals (see Stoet & Snyder, 2004). For each neuron, we determined whether the spike rate reflected the presence of incongruity in the period from 25 to 225 msec following stimulus onset. We calculated the fraction of cells that were significantly more active following an incongruent stimulus. This fraction was not significantly different from chance (3.7%), and was similar to the fraction of significantly less active cells (3.9%). The mean activity at the population level (±standard error) was exactly the same for incongruent and congruent stimuli (15.7 ± 0.7 sp/s). Similar results were obtained when we considered different time intervals (e.g., 50–250 msec, 100–300 msec, and 50–350 msec after stimulus

Table 1. Mean Reaction Time (msec), Movement Time (msec), Saccade Reaction Time (msec), and Percentage of Errors in Congruent and Incongruent Conditions for Two Monkeys

	RT		*MT*		*SRT*		*Errors*	
Animal	*M1*	*M2*	*M1*	*M2*	*M1*	*M2*	*M1*	*M2*
Congruent	279	276	87	88	186	217	1%	2%
Incongruent	289	292	106	107	197	227	8%	14%
Difference	10	16	18	19	11	10	7%	12%

All comparisons between congruent and incongruent conditions were tested for significance using Student's *t* tests for RT, MT, and SRT, and χ^2 tests for the error rates. All comparisons reached significance ($p < .05$).

RT = reaction time; MT = movement time; SRT = saccade reaction time; PE = percentage of errors.

onset). Thus, we could not establish a general effect of stimulus congruence on neuronal activity at either the single neuron level or at the population level in the PPC.

Although we found no significant effects of congruence on the amplitude of the neuronal activity, there might be specific effects of congruence on spatially tuned responses. Spatially tuned neurons are common in the PPC (Snyder, Batista, & Andersen, 2000; Colby & Goldberg, 1999; Andersen, Essick, & Siegel, 1985), but the interpretation of spatial tuning is still a matter of considerable investigation and debate (see below). The interaction of incongruity with spatial tuning may help to shed light on this issue.

Tuned spatial responses occurring around the time of a motor response may reflect a motor command for execution (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975), or they may reflect an efference copy of a command that has been generated elsewhere (von Holst & Mittelstaedt, 1950). If the spatially tuned activity substantially precedes the motor output, then it may reflect a sustained sensory response (Duhamel, Colby, & Goldberg, 1992), a neural correlate of covert attentional processes (Bushnell, Goldberg, & Robinson, 1981), a neural correlate of motor intention (Snyder, Batista, & Andersen, 1997, 2000), or a decision variable related to the value of either a particular stimulus or a particular response (Sugrue, Corrado, & Newsome, 2004; Platt & Glimcher, 1999).

The effect of congruence on neuronal latency can illuminate the nature of the neural response. The latencies of spatially tuned neural responses (henceforth ''spatial-response latencies'') may be unaffected by whether a stimulus is congruent or incongruent. This would suggest that spatially tuned neural responses reflect low-level sensory properties that are extracted prior to any task-specific processing. An effect of stimulus congruence on spatial-response latency that is equal to the effect of congruency on behavioral response latency (i.e., a response delay of 10–16 msec on congruent compared to incongruent trials) would be consistent with a motor command or an efference copy of a motor command. An intermediate effect of stimulus congruence would be consistent with a cognitive intermediate such as a valuation of a particular stimulus or response, or with a mixture of sensory, motor, and cognitive signals, as might occur at an intermediate stage of processing.

In order to investigate this, we first identified cells that were directionally tuned, that is, cells whose activity was correlated with reaches toward either the right or the left response button. For each of the 378 cells, we compared spike rates in the interval starting 200 msec before response onset until 100 msec after response onset. We found that the firing rates of 62% of cells (233 out of 378) were significantly different for left and right responses (Student's t test, alpha level of 5%). This percentage may underestimate the prevalence of directional tuning in the PPC because we did not adjust the position of the response button on a cell-by-cell basis.

Next, we determined the effect of stimulus congruence on the timing of neuronal responses. In Figure 2, we show a cell that shows higher firing for reaches to the left compared to the right (solid vs. dotted traces). In this cell, the divergence in firing rate occurred sooner for congruent trials than for incongruent trials (dark gray

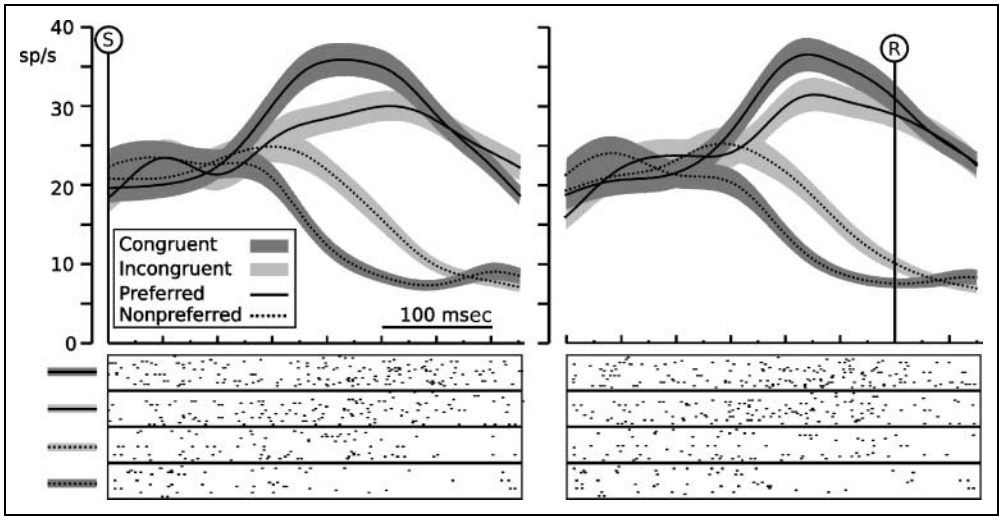

Figure 2. Neuron showing delayed spatial response latency due to stimulus incongruity. Data aligned on the onset of the imperative stimulus (S) on left and on the onset of the reaching response (R) on the right. The cell was spatially responsive and fired more vigorously when the monkey reached for the left response button than for the right (average spike rate and standard error are displayed). 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 (dotted 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).

vs. light gray traces). We quantified neuronal response timing in two ways. First, we computed spatial-response latencies, which we defined as the time at which firing on preferred and null direction trials first differed significantly from one another (see Methods). Because activity changes slowly at the time of response onset, small differences in activity can lead to large differences in apparent response latency. We therefore used a second, more reliable method to quantify differences in neuronal timing: We compared the times at which the population-averaged activity (preferred vs. nonpreferred response) achieved half of its maximum difference in firing rate. In the case of the example cell (Figure 2), we found a difference in latency between congruent and incongruent conditions of 41 msec and a difference in half-maximum values of 55 msec.

The data from individual cells were often noisy. Therefore, we chose the following method of analysis. We performed a millisecond by millisecond subtraction of firing rate when the response was made in the preferred minus the nonpreferred direction. In other words, in Figure 2, we would subtract the dashed lines from the corresponding solid lines. The resulting data isolate the directional component of the response. We then averaged across cells and smoothed the data (low-pass filter, −3 dB point of 9 Hz). This analysis (Figure 3A) showed 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%; $p > .1$) reduction in the maximum amplitude of direction-related activity, which occurred ∼350 msec after stimulus onset.

The spatial-response latencies were 90 msec on trials with congruent stimuli and 113 msec on trials with incongruent stimuli. Because the neuronal activity precedes the corresponding mean saccadic latencies (202 and 217 msec, respectively) by over 100 msec, the activity is unlikely to reflect an efference copy of the saccade command or a visual reafference response. The difference between congruent versus incongruent neural response latencies approached but did not reach significance ($p < .08$, Monte Carlo test; see Methods). However, this same difference was highly statistically significant when a more robust measure of timing was used: Half-maximum activity was achieved 196 and 224 msec after stimulus onset for congruent and incongruent stimuli, respectively ($p < .0003$, Monte Carlo test). The latency difference identified by the two methods was similar (23 and 28 msec), although variability was substantially less for the latter measurement.

We asked the same question while aligning on response onset instead of imperative stimulus onset (Figure 3B). Again, we found that the divergence occurred sooner in time (by 19 msec, $p < .08$) and that the half-maximum value also occurred sooner in time (by 18 msec, $p < .001$) in the congruent compared to the incongruent condition.

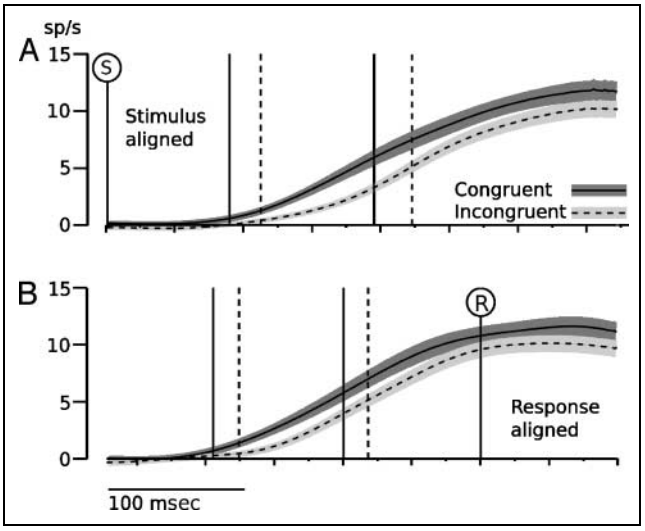

Figure 3. The timing of the directional response of the population of directionally selective neurons from both animals. For each cell the trials were sorted by the direction of the reach. Responses on null direction reaches were subtracted from responses on preferred direction reaches. The data were 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 (see Methods). (A) Data aligned on the onset of the imperative stimulus. The population response to congruent stimuli starts earlier (90 msec after stimulus onset, left solid line) than the response to incongruent stimuli (113 msec after stimulus onset, left dashed line). The difference in timing is similarly reflected in the time to half-maximum activity (196 msec for congruent stimuli, right solid line, and 224 msec for incongruent stimuli, right dashed line). (B) Data aligned on the onset of the arm response. The population response to congruent stimuli starts earlier (197 msec before response onset, left solid line) than the response to incongruent stimuli (178 msec 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 msec for congruent stimuli, right solid line, and −83 msec for incongruent stimuli, right dashed line).

In order to explore this result further and to explore the possibility that cells that maintain task information may play a different role in stimulus–response mapping than cells that do not maintain task information, we decided to separately analyze cells with and without task information ($TASK^+$ and $TASK^-$ cells; see Methods for definition).

We began by asking whether there is an interaction between the encoding of information related to task and the encoding of information related to response direction. We compared the timing of directional responses for congruent and incongruent trials in cells that encode task information ($TASK^+$) with the timing of directional responses in those cells that do not encode task information ($TASK^-$). For each cell, we performed a millisecond by millisecond subtraction of firing rate in the preferred and nonpreferred response conditions, and then averaged the result across neurons. Effects in cells

preferring the color task (n = 37) and the orientation task (n = 40) were similar, and therefore, these two subpopulations of cells were pooled.

We expected that a population of cells representing a motor variable (including an efference copy signal) would show a neuronal effect of congruency that was matched to the behavioral effect. Using the same methods as described previously, we found a 15 msec slowing of the time to half maximum (215 vs. 230 msec) in TASK$^-$ cells (Figure 4A). A Monte Carlo test showed that the difference in neuronal timing for congruent versus incongruent stimuli was highly significant ($p < .007$). The close match between the cost of incongruity in behavior (10–16 msec) and in the neuronal measure (15 msec) strongly suggests that TASK$^-$ cells encode a variable closely related to the motor response. The same analysis, but applied to data aligned on response onset instead of imperative stimulus onset, revealed a similar time to half-maximum activity of 5 msec (Figure 4B; $p < .01$).

For TASK$^+$ cells, the effect of congruence on neuronal timing was very different (Figure 4C). The time to half-maximum activity was slowed by 49 msec in the incongruent condition (164 vs. 213 msec; difference significant at $p < .0004$ by a Monte Carlo analysis). This ~50-msec difference in response time is apparent in the onset time as well (Figure 4C and D). Thus, the TASK$^+$ cells, unlike the TASK$^-$ cells, show a much larger effect of congruence (~50 msec) than the earliest motor responses (15 msec difference in saccade latency). We found similar results when aligning on response onset instead of on imperative stimulus onset: The time to half-maximum activity was slowed by 32 msec in the incongruent compared to the congruent condition ($p < .01$). In other words, parietal task neurons "solve" the stimulus–response mapping sooner on congruent compared to incongruent trials, even when the neuronal data are aligned on the motor response. These results disassociate the activity of TASK$^+$ cells from sensory variables (which would be expected to show no difference in timing relative to imperative stimulus onset) as well as from motor variables (which would be expected to show no difference in timing relative to response onset).

The large effect of congruence on the timing of the population TASK$^+$ cell response was not driven by a small number of outliers, but instead reflects the behavior of most cells. Figure 5 shows the half-maximum times for individual TASK$^+$ and TASK$^-$ cells under congruent (x-axis) and incongruent (y-axis) conditions. Like the population-averaged response, most individual TASK$^+$ cells reached half-maximum time faster in the congruent than in the incongruent condition [$\chi^2(1) = 5.0$, $p < .02$]. For the TASK$^-$ cells, we found no significant difference [$\chi^2(1) = 0.8$, $p > .3$]. These results show that the ~50 msec lead in the population-averaged

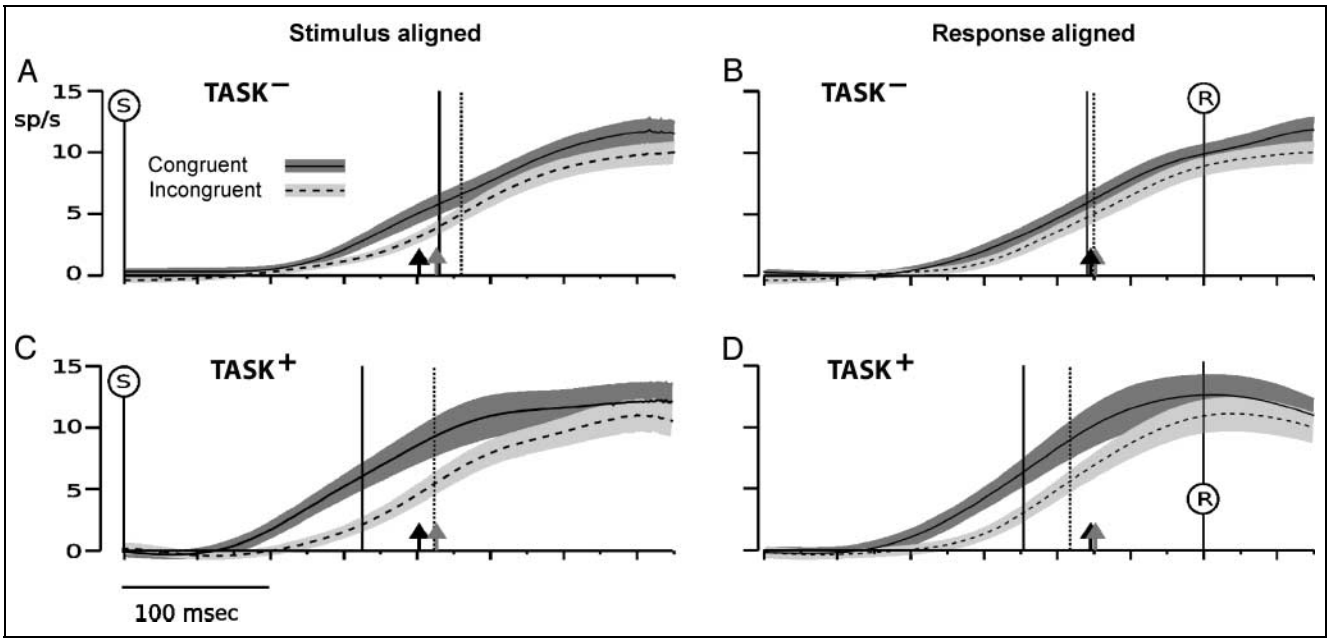

Figure 4. Onset of neural directional response (preferred minus nonpreferred direction) as a function of task selectivity and imperative stimulus congruency. (A) The difference in the time to half-maximum activity for congruent trials (215 msec, solid vertical line) and incongruent trials (230 msec, dashed vertical line) is similar to the behavioral response latency difference. Average saccade response times are indicated by black (congruent) and gray (incongruent) arrows. (B) Same data as in panel A, but now aligned on arm response onset. Latency difference between congruent trials (−80 msec) and incongruent trials (−75 msec) is very small (5 msec). (C) Similar to panel A, but for the TASK$^+$ cells. In contrast to the TASK$^-$ cells, there is a large latency difference in the time to half-maximum activity between congruent (164 msec) and incongruent trials (213 msec). (D) Similar to panel B, but for the TASK$^+$ cells. Latency difference between congruent trials (−123 msec) and incongruent trials (−91 msec) is 32 msec.

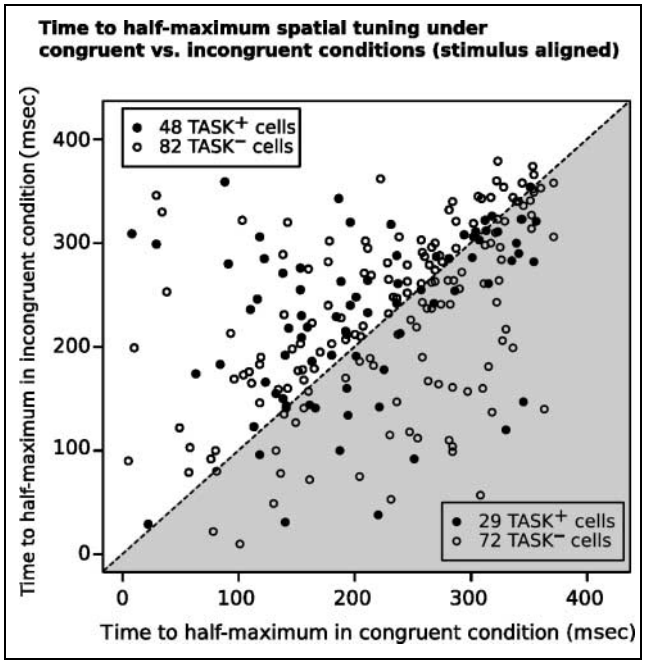

Figure 5. Time to half-maximum activity from individual cells. Significantly more $TASK^+$ cells showed longer times to half-maximum activity under incongruent compared to congruent conditions, but this was not the case for $TASK^-$ cells. Three cells had identical half-maximum times for congruent and incongruent conditions and are not included in the cell counts shown on the figure.

response of $TASK^+$ cells to congruent compared to incongruent stimuli is a property exhibited by many individual posterior parietal cells.

DISCUSSION

We investigated the responses of neurons in the PPC in a task-switching paradigm in order to gain insight into how the brain uses contextual information to process sensory stimuli in a task-appropriate manner, and to determine whether spatially tuned responses in the PPC reflect sensory, cognitive, or motor processes. We compared trials using congruent stimuli (those stimuli which require the same response in the two tasks) with trials using incongruent stimuli (those stimuli which require different responses in the two tasks). In this and in a previous study (Stoet & Snyder, 2003a), we found that monkeys, like humans, respond more slowly and less accurately to incongruent stimuli.

Brain imaging studies of the human PPC reveal an increased BOLD signal following incongruent stimuli (Adleman et al., 2002; Peterson et al., 1999; Taylor et al., 1997; Carter et al., 1995; Bench et al., 1993). 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), whereas our study used a nonverbal task. It is possible, for example, that the involvement of the human parietal cortex in conflict depends on the type of task this conflict occurs in (e.g., verbal vs. nonverbal tasks). 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 measure different quantities, and the results of the two methods may not be directly comparable. BOLD signals are imperfectly correlated with measures of neuronal electrical activity (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001).

We found a surprising result when comparing the neuronal response during congruent and incongruent trials. Because incongruent stimuli are associated with longer behavioral reaction times, it was not surprising to find that the neuronal latencies to encode response-related information were faster on congruent compared to incongruent trials. In $TASK^-$ cells, the consequence of incongruity on neuronal latency was very similar to the effect on behavior (15 msec vs. 10–16 msec, respectively). This is also reflected in the observation that $TASK^-$ cell responses under congruent compared to incongruent conditions overlap one another when aligned on response onset (Figure 4B). In contrast, $TASK^+$ cells showed a neuronal effect of incongruity that was much larger than the behavioral effect (49 msec vs. 10–16 msec, respectively). This can be seen by the fact that $TASK^+$ cell responses under congruent and incongruent conditions do not overlap one another when aligned either on the time of stimulus appearance or on the time of the motor response (Figure 4C and D, respectively). Furthermore, by comparing the upper and lower halves of Figure 4, it can be appreciated that $TASK^+$ cells encode the animal's upcoming choice regarding where to move sooner than $TASK^-$ cells, especially on congruent trials.

These results have important implications. The fact 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 & 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 $TASK^-$ cells carrying either a motor command signal

(Mountcastle et al., 1975) or an efference copy signal (von Holst & Mittelstaedt, 1950).

Furthermore, by isolating the responses of $TASK^+$ and $TASK^-$ cell populations, we are able to see that monkeys do not respond as soon as parietal neurons encode a decision. Instead, button presses on difficult (incongruent) trials are delayed relative to button presses on easy (congruent) trials. What could explain the fact that $TASK^+$ cells encode the correct response on congruent trials nearly 50 msec sooner than on incongruent trials, and yet the behavioral cost of stimulus incongruity is only 10–16 msec? Or, put differently, why don't monkeys respond still faster to congruent stimuli, given that their parietal cortices encode the correct response so quickly? One possibility is that, in the presence of conflict, animals use a more stringent criteria before responding. Another possibility is that the parietal cortex is only one of several brain areas performing this sensory to motor computation, and that the other areas arrive at the correct response much more slowly than the parietal cortex.

We have been referring to $TASK^+$ and $TASK^-$ cells as members of two discrete populations. It is quite possible that they instead reflect two ends of a continuum. The fact that $TASK^+$ and $TASK^-$ cells are intermixed within the same set of anatomical regions supports the idea of a continuum (Stoet & Snyder, 2004). However, whether $TASK^+$ and $TASK^-$ cells represent two distinct populations or the ends of a continuum does not substantially alter the conclusion that cells that encode task information also play a different role in sensory to motor processing than cells that do not encode task information, and furthermore, that the role played by a subset of PPC neurons cannot be described as simply representing sensory impressions or motor commands.

The implications of this study go beyond understanding task-specific processing in simple cognitive tasks. Context-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 which immediately precede or immediately follow it (Strohner & Stoet, 1999; Gerrig & Murphy, 1992). It is intriguing to try to identify the origins of human language skills in the abilities of present-day nonhuman primates (Ujhelyi, 1996; Premack, 1971; Gardner & Gardner, 1969), and to determine whether these origins might involve the PPC and its role in context-specific processing (Gurd et al., 2002).

In summary, the current article provides additional support for the idea that single neurons in the PPC represent abstract task information and play a central role in using contextual information to help map sensory stimuli onto motor outputs. More generally, this article adds to the growing body of evidence that single neurons in the PPC function as task-specific processing agents (Stoet & Snyder, 2004; Assad, 2003; Calton, Dickinson, & Snyder, 2002; Toth & Assad, 2002; Snyder et al., 1997, 2000).

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