

# Orienting Attention in Time Activates Left Intraparietal Sulcus for Both Perceptual and Motor Task Goals

Karen Davranche<sup>1</sup>, Bruno Nazarian<sup>2</sup>,  
Franck Vidal<sup>1</sup>, and Jennifer Coull<sup>1</sup>

## Abstract

■ Attention can be directed not only toward a location in space but also to a moment in time (“temporal orienting”). Temporally informative cues allow subjects to predict when an imminent event will occur, thereby speeding responses to that event. In contrast to spatial orienting, temporal orienting preferentially activates left inferior parietal cortex. Yet, left parietal cortex is also implicated in selective motor attention, suggesting its activation during temporal orienting could merely reflect incidental engagement of preparatory motor processes. Using fMRI, we therefore examined whether temporal orienting would still activate left parietal cortex when the cued target required a difficult perceptual discrimination rather than a speeded motor response. Behaviorally, temporal orienting improved accuracy of target identification as well as speed of target detection, demonstrating

the general utility of temporal cues. Crucially, temporal orienting selectively activated left inferior parietal cortex for both motor and perceptual versions of the task. Moreover, conjunction analysis formally revealed a region deep in left intraparietal sulcus (IPS) as common to both tasks, thereby identifying it as a core neural substrate for temporal orienting. Despite the context-independent nature of left IPS activation, complementary psychophysiological interaction analysis revealed how the functional connectivity of left IPS changed as a function of task context. Specifically, left IPS activity covaried with premotor activity during motor temporal orienting but with visual extrastriate activity during perceptual temporal orienting, thereby revealing a cooperative network that comprises both temporal orienting and task-specific processing nodes. ■

## INTRODUCTION

Various studies have examined the psychophysical and neural bases of directing, or “orienting” attention to locations in space, most notably using the spatial orienting paradigm developed by Posner, Snyder, and Davidson (1980). Adapting this classic paradigm for the temporal domain, Coull and Nobre (1998) demonstrated that attention could also be voluntarily oriented to specific moments in time (“temporal orienting”). In the orienting paradigm, spatially or temporally informative cues allow subjects to predict where or when an imminent target will appear, thereby speeding RTs as compared with neutral, uninformative cues. Neuroimaging data (PET and fMRI) revealed hemispheric lateralization for spatial and temporal orienting in right and left inferior parietal lobes, respectively (Coull & Nobre, 1998).

These data may seem at odds with many studies showing timing-related activity in a distributed cortico-striatal network, including SMA, right inferior frontal cortex, and BG (e.g., Harrington, Zimelman, Hinton, & Rao, 2010; Livesey, Wall, & Smith, 2007; Coull, Vidal, Nazarian, & Macar, 2004; Ferrandez et al., 2003). However, these studies typically employ explicit timing tasks, in which subjects

compare the duration of a currently elapsing sensory event with that of a previously memorized standard to make overt judgments of relative duration (e.g., shorter or longer). By contrast, in the orienting paradigms associated with left parietal activity, subjects use temporal cues to direct attentional resources to precise moments in time so as to optimize sensorimotor processing of events appearing within this attentional window, resulting in faster responding (Coull & Nobre, 1998) or more accurate discrimination (Correa, Lupiáñez, & Tudela, 2005). Interestingly, however, if temporal cues are used to make overt duration judgments (e.g., did the event occur earlier or later than expected) then areas typical of explicit timing tasks, such as cerebellum and right-sided cortical areas, are found once more (O’Reilly, Mesulam, & Nobre, 2008). Recent meta-analyses confirm that whereas a distributed cortico-striatal network is associated with explicit duration judgments (Wiener, Turkeltaub, & Coslett, 2010a), left parietal cortex is associated with the use of temporal cues to optimize (nontemporal) processing at predictable moments in time (Wiener, Turkeltaub, & Coslett, 2010b).

Yet left inferior parietal cortex has also been implicated in motor orienting of attention (or “motor intention”; Rushworth, Ellison, & Walsh, 2001), in which subjects are cued to respond to a target with a particular motor effector. Such neuroanatomical overlap suggests that

<sup>1</sup>Université de Provence and Centre National de la Recherche Scientifique, <sup>2</sup>Centre Hospitalier Universitaire de La Timone

activation of left inferior parietal cortex by temporal orienting may simply be an incidental consequence of selective motor attention. This hypothesis is unlikely to provide a complete explanation, however, given that left inferior parietal cortex is still activated by temporal orienting even when subjects cannot prepare in advance the side (left or right) of the eventual motor response nor indeed the motor effector system (eyes or hands) with which the response will be made (Cotti, Rohenkohl, Stokes, Nobre, & Coull, 2011). Nevertheless, to confidently reject the null hypothesis that left parietal activation during temporal orienting indexes incidental motor preparation processes, it would be helpful to show that left parietal cortex can still be activated by temporal orienting even when the cued target requires a nonmotor form of information processing.

Consequently, we conducted a block design fMRI study to compare and contrast neural substrates of perceptual versus motor versions of the temporal orienting task. Prior behavioral studies have confirmed that temporal orienting not only confers faster motor response times (Griffin, Miniussi, & Nobre, 2001; Coull & Nobre, 1998) but also enables faster and more accurate stimulus perception (Correa et al., 2005; Martens & Johnson, 2005; Correa, Lupiáñez, Milliken, & Tudela, 2004). We hypothesized that, if left inferior parietal cortex plays a fundamental role in temporal orienting, activation of this brain area should be observed whether the task was motor or perceptual in nature. The principle aim of this study was, therefore, to confirm the role of left inferior parietal cortex in the *perceptual* benefits of temporal orienting and to compare this directly to the motor benefits of temporal orienting within the same experimental paradigm. Previously, we (Coull & Nobre, 2008) and others (Assmus, Marshall, Noth, Zilles, & Fink, 2005; Assmus et al., 2003) have linked left inferior parietal cortex activity to the spatio-temporal predictability of dynamic stimuli when making perceptual collision judgments. A supplementary aim was, therefore, to confirm these findings within an entirely nonspatial context.

A final aim was to explore the physiological mechanisms underlying temporal orienting. Simply demonstrating that left inferior parietal cortex is activated by temporal cues does not tell us *how* these cues exert their performance-enhancing effects. One possibility is that, in a manner analogous to feature and spatial attentional mechanisms (Pessoa, Kastner, & Ungerleider, 2003), left inferior parietal cortex exerts top-down temporal attentional modulation of activity in task-specific networks. To test this hypothesis, we used psychophysiological interaction (PPI) analysis to determine whether the areas coactivated with left inferior parietal cortex changed significantly as a function of task context. Specifically, we predicted increased functional connectivity between left inferior parietal cortex and visual areas during perceptual discrimination, but between left inferior parietal cortex and motor areas during motor detection.

## METHODS

### Subjects

Thirteen healthy (three women) right-handed volunteers (mean age = 30 years,  $SD = 8$  years) participated in the study. The experimental protocol was approved by the local ethics committee, and written informed consent was obtained before the study. Although data from two additional subjects were acquired, they had to be discarded because of technical problems during stimulus presentation.

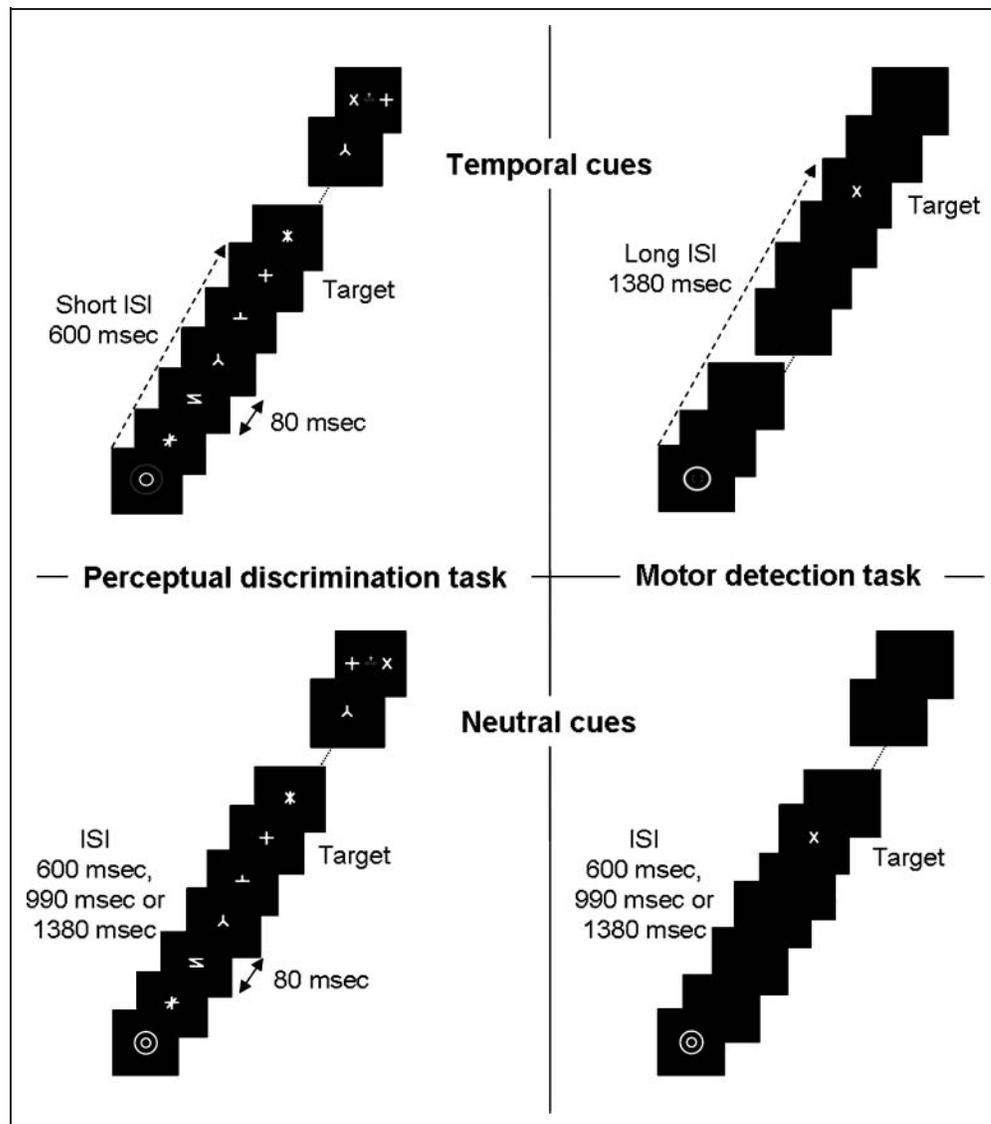
### Cognitive Tasks

Subjects were asked to perform a speeded motor detection and a perceptual discrimination version of a temporal orienting task. There were two cueing conditions per task, which manipulated subjects' expectations of when a target would appear: (i) the time condition, in which visual cues predicted the target would appear after either a short (600 msec) or long (1380 msec) cue-target ISI, and (ii) the neutral condition, in which visual cues provided no information concerning the length of cue-target ISI, which could be short (600 msec), medium (990 msec), or long (1380 msec). We, thus, had four conditions within a  $2 \times 2$  factorial design, with Task (Motor/Perceptual) and Cue (Time/Neutral) as the experimental factors (see Figure 1).

The basic visual display consisted of a black screen, in the center of which cues, distractors, and/or target stimuli appeared. Intertrial intervals varied between 500 and 1500 msec to prevent temporal anticipation of the next trial and to ensure random subsampling of the brain volume relative to each of the event types. Each trial began with a visual cue consisting of two concentric circles, presented for 500 msec (Figure 1). In the time condition, either the inner or outer circle could be brighter, indicating that the target would appear after a short (600 msec) or long (1380 msec) interval, respectively. The temporal information provided by the informative cue was 100% valid (i.e., the target always appeared at the predicted time), and short and long cue-target ISI trials were equiprobable.

In the neutral condition, the entire cue brightened, thus conveying no predictive information concerning cue-target ISI. The target could appear after a short (600 msec), a medium (990 msec), or a long (1380 msec) time interval. The medium length ISI was included to increase the uncertainty of target appearance at the longest interval, so as to minimize the asymmetric cueing benefits that are commonly seen in paradigms employing only two possible ISIs (Correa, Lupiáñez, & Tudela, 2006; Griffin et al., 2001; Coull, Frith, Buchel, & Nobre, 2000). In these paradigms, temporal cues typically speed RTs at short, but not long, ISIs (or "foreperiods" as they are sometimes called). This asymmetry is due to the predictive power of the unidirectional flow of time itself (Coull, 2009): If the target has not occurred at the short ISI in the neutral condition, then it must occur at the long one, allowing subjects to reorient attention to the long ISI, thus speeding performance. The

**Figure 1.** In the time conditions (top), a brighter inner circle (top left) predicts a short temporal delay before the onset of an upcoming target (600 msec), whereas a brighter outer circle (top right) indicates that the target will appear after a long interval (1380 msec). The figure shows illustrative examples only: In reality, both short and long cue types were intermixed during both the motor detection and perceptual discrimination tasks. In the neutral conditions (bottom), the entire cue brightened, providing no temporal information, and the target could appear after a short (600 msec), a medium (990 msec) or a long (1380 msec) time interval. Subjects provided a speeded motor response to the target in the motor detection tasks (right) but provided a delayed discriminatory response (left/right) of the symbols on the response screen of the perceptual discrimination task specified the response (index/middle finger) to be given and varied on a trial-by-trial basis. In the examples given here, the correct response would be a middle finger button press for the time condition (top left) and an index finger button press for the neutral condition (bottom left).



increasing conditional probability of event occurrence over time, the so-called “hazard function,” effectively removes the cost of the uninformative neutral cue, rendering the RT difference between temporally and neutrally cued trials at the long ISI negligible. Indeed, the neutral condition in the temporal orienting paradigm is akin to a variable foreperiod paradigm, in which RTs have repeatedly been shown to get faster as ISI gets longer (Niemi & Näätänen, 1981; Woodrow, 1914).

To minimize the behavioral consequences of the hazard function further still, we applied a probability bias to the distribution of the short, medium, and long ISIs. Specifically, they followed a “nonaging” distribution (e.g., Granjon, Requin, Durup, & Reynard, 1973; Baumeister & Joubert, 1969; Zahn & Rosenthal, 1966), with the probability of occurrence corresponding to 0.53, 0.27, and 0.13, respectively. This positively skewed a priori probability offsets the predictive power of the passage of time, rendering conditional probability effectively constant across the en-

tire ISI period. Finally, we also included a small number of catch trials (6.66%), in which no target was presented, to further increase uncertainty at the longest ISI as well as to prevent anticipatory responding in the motor task. Subjects were informed that no response was required during such trials.

Before fMRI scanning, all subjects performed a training session consisting of six blocks of 60 trials. Three blocks (two blocks of the time condition and one block of the neutral condition) of each task (motor detection or perceptual discrimination) were performed during this session.

#### *Motor Detection Task*

In the motor detection task (Figure 1, right), subjects were asked to respond, as quickly as possible, by pressing the response button with the right index finger as soon as the target symbol X appeared at the center of the screen.

Subjects were explicitly advised to use the temporal cues to predict when the target would appear so as to react to it as quickly as possible. They were told that neutral cues did not allow them to predict when the target would appear but that they should still try to respond as quickly as possible whenever it appeared.

### *Perceptual Discrimination Task*

In the perceptual discrimination task (Figure 1, left), subjects were asked to discriminate which of two target symbols (+ or ×) had been presented within a rapid serial presentation of visually similar distractors. Our paradigm was modeled on that used by Correa et al. (2005). The visual stream (2083 msec) comprised rapid presentation (50 msec presentation time per symbol, ISI = 83.33 msec) of 14 distractors, which had been randomly selected from a set of six possible symbols, plus one target. One of two target symbols could appear, once only, in either the fifth, eighth, or eleventh position of the stream, corresponding to an ISI of 600, 990, and 1380 msec, respectively. Subjects were asked to use the temporal cue to predict when the target would appear in the sequence so as to better discriminate which of the two target symbols (+ or ×) had been presented. On the other hand, they were informed that neutral cues could not help them predict when the target would appear but that they should still try to discriminate target shape.

In contrast to the motor detection task and to minimize the motor component of the perceptual discrimination task, subjects did not respond as soon as they had seen the target but instead had to wait until the offset of the visual stream, at which point a response screen was presented for 2000 msec. They were under no time pressure to give a response and were aware that only the accuracy of the response would be taken into account. Crucially, the onset of the response screen was identical across time and neutral conditions, meaning that the timing of the discriminatory response was no more predictable in the time condition than in the neutral condition. As previously described, the only item that was differentially predictable across conditions was the onset of the target to be discriminated.

Upon presentation of the response screen, subjects had to press one of two response buttons corresponding to which of the two targets had been perceived during the sequence. The response screen presented the two possible targets (+ and ×), one on the left-hand side and one on the right-hand side of the screen. If the perceived target appeared on the left-hand side, the subject pressed with their index (leftmost) finger of the right hand, whereas they pressed with their middle (rightmost) finger of the right hand if it appeared on the right-hand side of the response screen. To minimize motor preparation as much as possible, the nature of the response signal changed from trial to trial: On half of the trials, the + appeared on the left of the screen and the × appeared on the right, whereas

these contingencies were reversed on the remaining trials (see Figure 1, left). In this way, subjects could not begin to prepare a motor response as soon as the target had been detected. Index and middle finger responses were counterbalanced across all conditions and trials. If participants failed to respond within 2000 msec, the response signal disappeared and the next trial began. During catch trials (6.66%), in which no target was presented, the response screen comprised two horizontal dashed lines (- -) in place of the + and × symbols and the subject made no response.

### **fMRI Scanning**

Scans were acquired using a 3-T (3T-MAGNEX) Bruker Medspec 30/80 Advance whole-body MRI system (Ettlingen, Germany), equipped with a head coil. EPI was used to obtain T2\*-weighted fMRI images in the axial plan, using an interleaved slice acquisition sequence. The acquired image volume consisted of  $36 \times 3$  mm transverse slices, with an interscan interval (TR) of 2.4 sec. The size of this image volume allowed us to scan the entire cerebral cortex and most of the cerebellum. Three scanning runs (339, 340, and 343 image volumes, approximately 13 min per run) were acquired for each subject.

The fMRI experimental design was blocked. Each scanning run contained five blocks (25–32 sec per block) of each of the four experimental conditions (motor time, motor neutral, perceptual time, and perceptual neutral). Each block contained six trials of the appropriate experimental condition, giving a total of 90 trials per experimental condition across the three scanning runs. The four experimental conditions were presented in permuted order. After one full permutation of the four conditions, a short (16 sec) baseline condition was inserted, which comprised a central fixation point (×) identical to the target used for the detection task. Subjects were asked simply to fixate the × during this time. A structural MRI was also acquired (using a standard T1-weighted scanning sequence, 1 mm<sup>3</sup> resolution) to allow anatomically specific localization of significant areas of brain activation.

### **Data Analysis**

#### *Behavioral Data*

Initially, we conducted a behavioral pilot study to validate the paradigm by verifying that both motor and perceptual performance could be improved by the use of temporal cues. Behavioral data were collected from 12 subjects (nine women, mean age = 33 years), although data from two subjects were discarded due to chance performance in the discrimination task (<50% of accuracy). The relative advantage of temporal cueing was assessed independently for the motor detection and the perceptual discrimination task, using repeated measures ANOVA with temporal

cueing (time vs. neutral) and ISI duration (short vs. long) as within-subjects factors. Significance was set at  $p < .05$  for all analyses. For the detection task, overt responses before presentation of the response signal, responses to catch trials, and anticipatory (RT < 100 msec) or exceedingly slow (RT > 1500 msec) responses were excluded from further RT analyses. For the discrimination task, the analysis was performed on accuracy data, corresponding to the percentage of correct target discriminations. As means and variances of percentage data are closely related, percentage accuracy data were arcsine transformed before being submitted to the ANOVA.

Additional analyses using signal detection theory, a more sensitive measure of perceptual performance, assessed whether temporal orienting differentially affected perceptual sensitivity and response criterion, indexed by  $d'$  and beta measures, respectively (Green & Swets, 1966). Mean  $d'$  and beta values were submitted to separate ANOVAs with temporal cueing (time vs. neutral) as a within-subject variable. Unfortunately, the number of trials was insufficient (particularly in the neutral condition because of the use of the nonaging distribution) to produce robust values for short and long trial types separately; therefore, we were unable to include ISI duration (short vs. long) as a second within-subject factors. Behavioral data collected during the brain imaging session were analyzed in an identical manner to assess the effect of temporal cueing on both detection speed and perceptual discrimination during fMRI acquisition.

### fMRI Data

Functional images were processed and analyzed with SPM5. All functional images for each subject were slice time corrected, then realigned to correct for head movement between scans. Each structural MRI was coregistered to the corresponding mean realigned functional image to put structural images into the functional brain space. All images were then spatially normalized into a standard spatial reference frame by matching each image to a standardized template from the Montreal Neurological Institute. Functional images were spatially smoothed to accommodate intersubject differences in anatomy using isotropic Gaussian kernels of 8 mm.

Condition and subject effects were estimated according to a general linear model at each voxel in brain space. We initially implemented 13 separate within-subject analyses. For each subject, we specified two contrast vectors to produce SPMs that identified regions activated by temporal orienting in either task by contrasting the condition in which cues conveyed temporal information with the condition in which they conveyed no temporal information ([Motor Time – Motor Neutral] or [Perceptual Time – Perceptual Neutral]).

Each of the 13 maps (one per subject) that had been defined for each contrast of interest were then entered into a second level of analysis, and statistical inferences for each

contrast were derived using one-sample (simple main effects) or paired (interactions)  $t$  tests in SPM. We identified (1) regions selectively recruited by temporal orienting during each task independently (i.e., the simple main effects of cue [Motor Time – Motor Neutral] and, separately, [Perceptual Time – Perceptual Neutral]), (2) regions preferentially activated by temporal orienting during one task compared with the other (i.e., the interaction between task and cue [Motor Time – Motor Neutral] – [Perceptual Time – Perceptual Neutral] and, conversely [Perceptual Time – Perceptual Neutral] – [Motor Time – Motor Neutral]), and (3) regions common to temporal orienting during both tasks (i.e., the conjunction of the simple main effect of cue in motor and perceptual tasks ([Motor Time – Motor Neutral] and [Perceptual Time – Perceptual Neutral])). To control for the large sensorimotor differences across tasks, the time conditions were first compared with their respective neutral conditions (simple main effects of cue) before then being compared with one another (Cue  $\times$  Task interaction). For reference purposes, the main effects of each task [(Motor Time + Motor Neutral) – (Perceptual Time + Perceptual Neutral)], and vice versa were separately assessed using one-sample  $t$  tests and are included in Supplementary Material. However, the main purpose of this investigation was to interrogate whether discrete components of these task-specific networks could be modulated by temporal attention, hence the contrasts comparing temporal to neutral cues (described above) form the basis of this report.

As previous findings in the literature (Coull, Nobre, & Frith, 2001; Coull & Nobre, 1998) allow us to define a specific region (viz. left inferior parietal cortex and IPS) within which to interrogate the data for simple main effects and interactions, we adopted a significance threshold for this region that was uncorrected for multiple comparisons ( $p < .001$ ). This region was further subject to a small volume correction procedure, thresholded at  $p < .05$  corrected (using false discovery rate) for multiple comparisons. The restricted search volume was defined as a spherical ROI, with a radius of 12 mm, centered on the mean coordinate (–36, –51, 45 mm) of previously reported (Coull et al., 2001; Coull & Nobre, 1998) activation peaks. Otherwise, all other regions were thresholded at  $p < .05$ , corrected (using false discovery rate) for multiple comparisons. In addition, we inclusively masked activations resulting from the Task  $\times$  Cue interaction analysis with the simple main effects of temporal cue for each task type (e.g., ([Motor Time – Motor Neutral] – [Perceptual Time – Perceptual Neutral]) was masked inclusively by [Motor Time – Motor Neutral] thresholded at  $p < .05$ , uncorrected for multiple comparisons). This procedure ensured that the activations reported for the interaction were due to temporal cueing in the task of interest rather than neutral cueing in the comparison task.

Additionally, we investigated task-related changes in functional brain connectivity using psychophysiological interactions (PPIs). The PPI analysis examines whether

region-to-region coactivation changes significantly as a function of task. Our physiological regressor was activity within the area of left parietal cortex specific to temporal orienting, the psychological regressor was the nature of the task (perceptual vs. motor) and the interaction between these two regressors represented the PPI. The seed area for the physiological regressor was defined in the following manner: The peak voxel location from the group conjunction map, corresponding to the brain area commonly involved in both motor and perceptual temporal orienting, was used to locate the nearest local maximum to the center of this volume in individual subject maps (i.e., the nearest single-subject peak to the coordinate  $[-33 -45 39]$ ). For each subject, we identified this peak within the contrast map that contained activity from both the motor and perceptual tasks (i.e., the main effect of temporal cueing  $[(\text{Motor Time} + \text{Perceptual Time}) - (\text{Motor Neutral} + \text{Perceptual Neutral})]$ , thresholded at  $p < .01$ ). We then defined a spherical VOI (12-mm radius) centered upon this peak. All single-subject VOIs lay within the 12-mm FWHM of the dataset and within a 12-mm radius from the group conjunction peak (with eight of the VOIs being centered exactly on this peak), apart from one subject whose VOI was centered 15 mm anterior to the group peak.

Using these subject-specific VOIs, eigenvariate time series were extracted from individual subject data to create one physiological regressor per run. These extracted data were used as inputs to whole-brain PPI analyses, along with the psychological regressor corresponding to task type (motor/perceptual) to generate individual subject PPI maps. A second level analysis was performed on individual PPI maps to investigate task-related changes in functional connectivity of left parietal cortex with any other area of the brain during temporal orienting in a motor or a perceptual context. PPI maps were thresholded at  $p < .001$  (minimum voxel extent 3).

## RESULTS

### Behavioral Data

#### *Behavioral Pilot Study*

During the motor detection task, RTs were faster when temporal cues were used (197 msec) than when neutral cues were provided (216 msec;  $F(1, 9) = 30.84, p < .001$ ). There was also a main effect of ISI duration ( $F(1, 9) = 5.76, p < .05$ ), such that RTs were faster for short ISIs (204 msec) than for long ones (214 msec). However, the interaction between the two factors was not significant.

For the perceptual discrimination task, signal detection theory revealed a significant perceptual advantage for temporal cues. Mean  $d'$  was higher ( $F(1, 9) = 11.88, p < .01$ ) when temporal (mean  $d' = 1.80$ ) rather than neutral (mean  $d' = 1.39$ ) cues were presented. The main effect of temporal cue on beta was far from significant ( $F < 1$ ).

Temporal cueing thus modulated perceptual sensitivity but not response criterion. We also examined percentage correct as a function of cue and ISI duration and found a significant interaction between temporal cue and ISI duration ( $F(1, 9) = 21.68, p < .01$ ). Specifically, temporal cues helped to correctly discriminate the target's appearance at the short ISI (a benefit of 8%,  $p < .01$ ) but not at the long one (a benefit of 1%,  $p = .19$ ). An asymmetric cueing benefit for short versus long ISIs is a common finding in temporal orienting tasks (Correa et al., 2006; Coull et al., 2000; Coull & Nobre, 1998) and is because of changing conditional probabilities of target appearance as a function of elapsing time (the "hazard function"; Niemi & Näätänen, 1981).

Overall, the results of the behavioral study validated the paradigm, showing that temporal cues improved both motor and perceptual behavior.

#### *fMRI Study*

Data collected during the brain imaging session confirmed the temporal cue advantage for the motor detection task ( $F(1, 12) = 36.28, p < .001$ ). RTs were faster when temporal cues were provided (344 msec) compared with neutral cues (383 msec). An interaction with ISI duration showed that this benefit tended to be greater ( $F(1, 12) = 4.17, p = .06$ ) for the short ISI duration (a benefit of 50 msec) than for the long one (a benefit of 28 msec). Temporal cues also improved accuracy of perceptual discrimination during the fMRI session. Specifically,  $d'$  was higher ( $F(1, 12) = 24.22, p < .001$ ) in the time condition (mean  $d' = 1.18$ ) than in the neutral condition (mean  $d' = 0.72$ ). By contrast, there was no effect of cueing on beta ( $F < 1$ ). The analysis of percentage correct at each of the ISIs showed improved performance with temporal cues at the short compared with long delay, although this effect did not reach a significant level ( $F(1, 12) = 2.05, p = .18$ ).

### fMRI Data

#### *Temporal Orienting Activity in Motor and Perceptual Tasks*

Analyzing the simple main effects of cue revealed that temporal, compared with neutral, cueing in the motor detection task selectively activated left parietal cortex, including both IPS and a more lateral region of inferior parietal cortex (Table 1A and Figure 2, top). Crucially, in the perceptual discrimination task temporal versus neutral cueing also revealed activation of left IPS (Table 1B and Figure 2, bottom). There were absolutely no other clusters of activity, even at a liberal threshold of  $p < .001$  (uncorrected for multiple comparisons).

The interaction between task type and cue, in which motor temporal cueing is compared directly to perceptual temporal cueing, revealed preferential activation of left IPS ( $[-33 -57 54] Z = 3.47$ ), left lateral inferior parietal cortex

**Table 1.** Temporal Orienting Activity, as Identified by the Contrast Time–Neutral, for (A) Motor and (B) Perceptual Versions of the Task, as well as Activity that is (C) Common to Both Motor and Perceptual Tasks

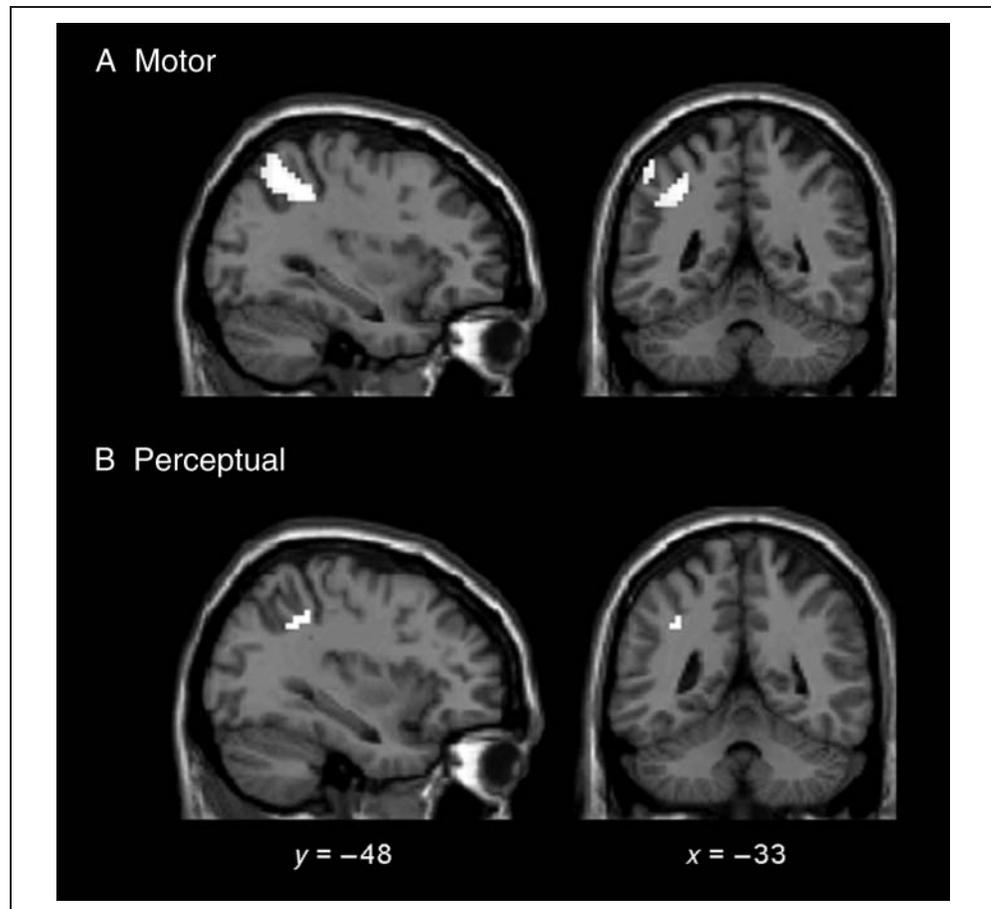
Anatomical Structure	<i>x, y, z Coordinates (mm)</i>	<i>Z score</i>
<i>(A) Motor Detection</i>		
L IPS	–36, –57, 48	4.23
	–45, –42, 36	4.08
L lateral inferior parietal cortex (BA 40)	–48, –51, 57	3.54
<i>(B) Perceptual Discrimination</i>		
L IPS	–33, –48, 36	3.32
<i>(C) Common to Motor Detection and Perceptual Discrimination</i>		
L IPS	–33, –45, 39	3.27

All activations were in hypothesized areas (left inferior parietal cortex and IPS; Coull & Nobre, 1998) and, therefore, significant at an uncorrected whole-brain threshold of  $p < .001$ . Supplementary small volume correction analysis further confirmed the significance of these areas at a corrected threshold of  $p < .05$ . L = left; BA = Brodmann's area.

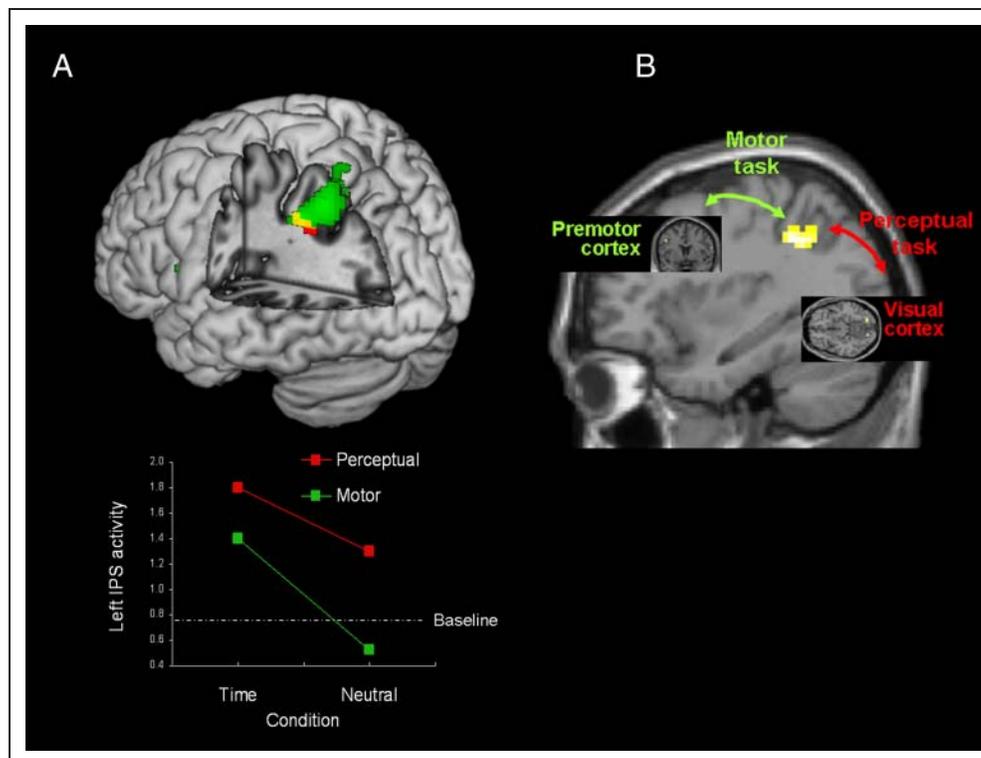
([–54 –48 48]  $Z = 3.55$ ), and left ventral premotor cortex ([–30 3 0]  $Z = 3.86$ ) for the motor versus perceptual version of the task. We also noted subthreshold activity selective to the motor temporal cueing in the right-sided

homologues of both inferior parietal cortex ([45, –60, 54]  $Z = 3.63$ ,  $p < .001$  uncorrected) and ventral premotor cortex ([39 0 24]  $Z = 4.15$ ,  $p < .001$  uncorrected). Although we had no a priori hypothesis that these right-sided areas

**Figure 2.** Left inferior parietal cortex is activated by temporal orienting (time–neutral) during both (A) motor detection and (B) perceptual discrimination tasks. Activations are displayed on coronal and sagittal sections of a coregistered template brain. The left side of the figure corresponds to the left side of the brain.



**Figure 3.** (A) Top: A task-independent temporal orienting area (yellow) is located in the left IPS, as revealed by the conjunction analysis of brain areas involved in motor (green) and perceptual (red) versions of the temporal orienting task. Bottom: Plot of brain activity (beta values) in this left IPS cluster [peak  $-33 -45 39$ ] showing greater activity in the time compared with neutral conditions for both motor and perceptual tasks. The dashed line indicates left IPS activity during the baseline condition. (B) Functional connectivity of left IPS changes as a function of task context. Activity in left IPS covaries with activity in extrastriate visual cortex during the perceptual discrimination task, but with activity in premotor cortex during the motor detection task.



would be activated by temporal orienting and, therefore, cannot formally treat them as significant at our uncorrected threshold, we report them here simply for completeness. No areas were significantly more activated by temporal cueing during the perceptual discrimination compared with motor detection task.

#### *Temporal Orienting Activity Common to Motor and Perceptual Tasks*

Conjunction analysis formally revealed that temporal orienting in both motor detection and perceptual discrimi-

nation tasks activated one region in common, namely left IPS (Table 1C and Figure 3A).

#### *Task-specific Patterns of Intraparietal Functional Connectivity*

PPI analysis revealed that functional connectivity of left IPS fluctuated as a function of the task (perceptual vs. motor). Specifically, the analysis revealed functional connectivity between left IPS and bilateral extrastriate visual cortex during the perceptual task. Conversely, we observed functional connectivity between left IPS and bilateral precentral

**Table 2.** PPI Results: Brain Areas Expressing an Interaction between Activity in Left IPS and the (A) Motor versus (B) Perceptual Nature of the Task

Anatomical Structure	<i>x, y, z</i> Coordinates (mm)	Z score
<i>(A) Motor Detection</i>		
R ventral premotor cortex (BA 6/44)	66, 0, 15	3.89
L inferior frontal gyrus (BA 44)	-45, 6, 33	3.41
L primary motor cortex (BA 4)	-30, -21, 57	3.88
<i>(B) Perceptual Discrimination</i>		
L fusiform gyrus (BA 18/19)	-15, -81, -12	3.78
R fusiform gyrus (BA 18)	27, -78, -12	3.48

All activations are significant at an uncorrected threshold of  $p < .001$ . L = left; R = right; BA = Brodmann's area.

and inferior frontal gyri during the motor task (Figure 3B and Table 2).

## DISCUSSION

The aim of this study was to investigate whether left inferior parietal cortex was consistently activated by temporal orienting whether temporal cues helped subjects make speeded motor responses or difficult perceptual discriminations. Analysis of behavioral data confirmed that temporal cues significantly enhanced both motor speed and perceptual sensitivity. Crucially, fMRI results confirmed that temporal orienting activated left inferior parietal cortex whether temporally informative cues were used to react more quickly or to optimize perceptual discrimination. Although the behavioral benefits of temporal orienting are now well established, this is the first neuroscientific demonstration that activation of left inferior parietal cortex during temporal attentional orienting is independent of task goals.

### Task-independent Activation of Left IPS by Both Motor and Perceptual Temporal Orienting

Left inferior parietal cortex is selectively activated both when subjects expect a target to appear at a particular moment in time (Coull & Nobre, 1998) or when they expect to provide a particular motor response (Rushworth et al., 2001; Rushworth, Nixon, Renowden, Wade, & Passingham, 1997). We, therefore, designed the present study to establish whether left inferior parietal cortex activity during temporal orienting tasks simply reflects the ability to prepare a *motor response* at a particular moment in time or, more generally, to direct attentional resources in time so as to optimize performance, whatever the nature of the task. First, we confirmed previous findings (e.g., Cotti et al., 2011; Coull et al., 2001; Coull & Nobre, 1998) that temporal orienting selectively activates left inferior parietal cortex when temporal cues are used to speed motor responding. Second, we show, for the first time, that temporal orienting also activates left inferior parietal cortex when temporal cues are used to help make difficult perceptual discriminations. Third, by comparing and contrasting neural substrates of motor and perceptual temporal orienting tasks within the same experimental paradigm (taking care to use a matched neutral cue condition to control for sensorimotor differences across tasks), we show that temporal orienting in both tasks activated the same region of left inferior parietal cortex, deep in the IPS, thus identifying this region as a core neural substrate for the orienting of attention in time, independent of task context.

We did note, however, subtle neuroanatomical differences according to the motor versus perceptual nature of the task: Although motor temporal orienting activated distinct areas of left IPS and adjacent lateral inferior parietal cortex, the activation was restricted to a single left IPS clus-

ter during perceptual temporal orienting (Figure 2). As discussed above, this pattern of results establishes left IPS as a core neuroanatomical substrate for temporal orienting but additionally suggests that the more lateral inferior parietal region is implicated more specifically in motor aspects of attentional orienting. Consistent with this hypothesis, lateral areas of left inferior parietal cortex, more precisely left supramarginal gyrus, have already shown to be implicated in the selection and preparation of hand movements independently of the lateralization (left/right) of the movement required (e.g., Hesse, Thiel, Stephan, & Fink, 2006; Astafiev et al., 2003; Rushworth, Johansen-Berg, Gobel, & Devlin, 2003; Rushworth et al., 2001). The lack of a more lateral parietal activation during the perceptual orienting task (Table 1) suggests that subjects did not use temporal cues to prepare the onset of a motor response in this task but, instead, to better discriminate a temporally defined target from surrounding visual distractors.

The interaction analysis revealed that temporal orienting induced subthreshold activations in right premotor and parietal cortices during the motor, but not perceptual, task. Although nonsignificant, these activations are worth mentioning given previous findings that motor versions of both spatial and temporal orienting engage an overlapping bilateral fronto-parietal network when compared with baseline (Coull & Nobre, 1998). However, spatial orienting was found to preferentially activate right parietal cortex when compared directly to temporal orienting, whereas temporal orienting preferentially activated left parietal cortex when compared directly to spatial orienting (Coull & Nobre, 1998). Therefore, although both hemispheres were recruited by both spatial and temporal orienting, each hemisphere was differentially sensitive to the spatial versus temporal characteristics of the task. Indeed, the greater specificity of left parietal cortex for temporal orienting is further supported by our current findings showing that left parietal cortex was the only region activated by both motor and perceptual versions of the task, whereas right parietal cortex was activated only (and at a subthreshold level) when the motor version was compared directly to the perceptual version. Therefore, although right parietal cortex may contribute to the distributed network of regions required to perform duration estimation (e.g., Buetti, Bahrami, & Walsh, 2008; Coull et al., 2004) or temporal orienting (Coull & Nobre, 1998), its involvement is not selective to either one of these. In addition, although some recent studies have demonstrated a selective role for right parietal cortex in timing, they have measured the temporal order of sequential events rather than the duration of a single event (VanRullen, Pascual-Leone, & Battelli, 2008; Battelli, Pascual-Leone, & Cavanagh, 2007).

### Relevance to Prior Studies of Temporal Predictability

In contrast to our consistently left-lateralized activations for temporal orienting (Cotti et al., 2011; Coull et al.,

2001; Coull & Nobre, 1998) others have highlighted a role for right PFC in temporal predictability (Buetti, Bahrami, Walsh, & Rees, 2010; Vallesi, McIntosh, Shallice, & Stuss, 2009; Vallesi, Shallice, & Walsh, 2007). Crucially, however, these studies measured temporal expectations that evolved as a function of the passage of time itself (the “hazard function”). In our temporal orienting studies by contrast, we measure expectations for a fixed moment in time that are derived a priori from learned visual cues (although see Triviño, Correa, Arnedo, & Lupiáñez, 2010, who have recently shown that an intact right PFC is necessary, but not specific, for temporal expectations derived either from the passage of time or from learned cues). In hazard function studies, subjects learn that a target can appear within a range of possible times and the expectation for target onset evolves dynamically within a single trial as a function of passing time. In the temporal orienting studies, on the other hand, subjects learn that a given cue indicates a particular onset time and so, within a single trial, expectations are fixed to the prelearned time.

Electrophysiological recordings of the contingent negative variation, a slow wave indexing temporal preparation, support the important distinction between expectations derived from the passage of time or those derived from learned cues. Specifically, when the contingent negative variation was measured over right frontal electrodes, it increased steadily until the end of the ongoing stimulus duration (Pfeuty, Ragot, & Pouthas, 2003), whereas if it was measured over left frontal (Pfeuty et al., 2003), parietal (Macar & Vidal, 2003), or premotor (Praagstra, Meyer, Cools, Horstink, & Stegeman, 1996) electrodes, it increased only up until the learned (or entrained) duration had been reached. This hemispheric distinction parallels previous fMRI data in which targets appearing at a delay later than expected, necessitating updating of expectations as a function of elapsed time, activated right frontal areas (Coull et al., 2000), whereas those appearing at previously learnt cued times activated left premotor and parietal areas (Coull & Nobre, 1998). Considered as a whole, these data suggest that right-sided cortical areas are critical for updating temporal expectations as a function of time-in-passing, whereas left parietal cortex is engaged when an overlearned temporal expectation is deployed in the first place.

### **Task-specific Functional Connectivity of Left IPS with Motor and Visual Processing Areas**

Conventional fMRI analyses provide information about the fluctuation of brain activity within a particular region as a function of the experimental manipulation. On the other hand, PPI analysis assesses correlations in activity between different brain areas and estimates how this correlation fluctuates according to experimental conditions. In the present study, this method was used to investigate how the functional connectivity of left IPS during temporal ori-

enting changes as function of the motor or perceptual nature of the task. As illustrated in Figure 3B, we observed that the level of activity in left IPS correlated over time with activity in bilateral premotor/motor cortex for the motor detection task and with activity in bilateral occipital cortex for the perceptual discrimination task. These differential patterns of interregional coactivation were consistent with distinct networks specific to the inherent characteristics of each cognitive task (motor vs. perceptual) and provided information, complementary to the results of the conventional analysis, concerning potential attentional mechanisms.

Merely attending to a specific stimulus feature, even in the absence of physical change, modulates activity in basic feature-specific visual processing areas (e.g., Pessoa et al., 2003; Kastner & Ungerleider, 2001; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990). In particular, modulation of feature- or sensory-specific activity by spatially directed attention has been the focus of a large body of work. Spatial attention affects neural activity through top-down inputs and biases information processing for stimuli appearing at the attended location (Kastner & Ungerleider, 2001). Functional brain imaging studies support the idea that this top-down spatial attention signal is generated by a distributed network of higher-order areas in frontal and parietal cortex (for a meta-analysis, see Kastner & Ungerleider, 2000). It is possible that analogous attentional control mechanisms may be activated during directed temporal orienting such that left IPS generates a top-down biasing signal for activity in task-specific sensorimotor areas (i.e., areas recruited for processing of specific stimulus features or motor task goals) so as to bias information processing for stimuli appearing at the cued time.

Electrophysiological recordings in nonhuman primates have shown that temporal expectancy modulates neuronal firing in ventral visual cortex during a feature discrimination task (Ghose & Maunsell, 2002) or in inferior temporal cortex during a perceptual temporal orienting task (Anderson & Sheinberg, 2008). In addition, very recent fMRI data demonstrate modulation of primary visual cortex activity by temporal expectancy in a speeded RT task (Buetti et al., 2010). Our own fMRI data reveal modulation of ventral occipital cortex by temporal expectancy during perceptual, but not motor, temporal orienting. The ventral visual (or “what”) pathway, projecting ventrally from primary visual cortex to inferior temporal cortex, is implicated in visual feature identification (Milner & Goodale, 1995; Mishkin, Ungerleider, & Macko, 1983). The lateral occipital complex in particular (located on the lateral bank of the fusiform gyrus extending ventrally and dorsally) plays a central role in human object recognition (Grill-Spector, Kourtzi, & Kanwisher, 2001; Kourtzi & Kanwisher, 2001; Malach et al., 1995). Coactivation of left IPS with lateral occipital cortex during temporally directed attention could, therefore, provide support for the notion that left IPS modulates activity in areas primordially engaged in the feature

discrimination aspects of our perceptual temporal orienting task.

In a similar vein, the motor intention literature shows that activity in motor processing areas can be modulated simply by anticipating that a movement will be executed, even in the absence of physical motor execution (Fabbri-Destro & Rizzolatti, 2008; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). This is a process perhaps equivalent to the attentional “baseline shift,” in which anticipation that a particular stimulus feature will be presented increases activity in feature-specific processing areas even before the stimulus has been physically presented (Chawla, Rees, & Friston, 1999; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). Covariation of left IPS with premotor cortex in our motor detection task suggests anticipatory modulation of premotor activity and is consistent with electrophysiological data showing modulation of motor cortex activity (either increased spike synchronisation [Riehle, Grun, Diesmann, & Aertsen, 1997] or increased firing [Renoult, Roux, & Riehle, 2006; Roux, Coulmance, & Riehle, 2003]) as a function of temporal expectancy in a choice RT task. Our premotor activity was localized to ventral premotor cortex (BA 6/44) bilaterally, considered the human homologue of monkey area F5 and anatomically connected to inferior parietal cortex (Luppino, Murata, Govoni, & Matelli, 1999). This circuit is critical in visuomotor transformations (Rizzolatti & Luppino, 2001) and has been implicated in the selection and preparation of hand movements (Rushworth et al., 2003; Toni, Rushworth, & Passingham, 2001). It is, therefore, conceivable that during motor tasks, temporally directed attention modulates activity in hand preparation areas, thus helping subjects to promptly perform the required manual motor act.

Yet, although functional connectivity analysis identifies regions that covary with one another, it does not specify the direction of influence. Therefore, the functional connectivity between left IPS and task-specific processing areas could instead represent a signal from visual or premotor cortices toward IPS. Elapsed time can be encoded within patterns of neural activity in context-specific processing areas (e.g., Mauk & Buonomano, 2004; Buonomano & Karmarkar, 2002). Therefore, in our perceptual temporal orienting task, the neural signature of elapsed time, instantiated in visual cortex (Bueti et al., 2010; Ghose & Maunsell, 2002), could signal when the cued time was reached and, therefore, activate attentional mechanisms in IPS. Parietal cortex may then, in turn, feedback into visual cortex so as to bias information processing. Given the lack of directionality in functional connectivity analysis, we cannot yet conclude whether our data represent a bottom-up or top-down mechanism, or indeed some combination of the two.

### Acknowledgments

This work was supported by the Agence Nationale de la Recherche ANR-07-NEURO-033-01 (awarded to J. T. C.). We thank Daniele Schön for discussion of data analysis.

Reprint requests should be sent to Jennifer Coull, Laboratoire de Neurobiologie de la Cognition, UMR 6155 Case C, Université de Provence, 3 place Victor Hugo, 13331 Marseille cedex 3, France, or via e-mail: jennifer.coull@univ-provence.fr.

### REFERENCES

- Anderson, B., & Sheinberg, D. L. (2008). Effects of temporal context and temporal expectancy on neural activity in inferior temporal cortex. *Neuropsychologia*, *46*, 947–957.
- Assmus, A., Marshall, J. C., Noth, J., Zilles, K., & Fink, G. R. (2005). Difficulty of perceptual spatiotemporal integration modulates the neural activity of left inferior parietal cortex. *Neuroscience*, *132*, 923–927.
- Assmus, A., Marshall, J. C., Ritzl, A., Noth, J., Zilles, K., & Fink, G. R. (2003). Left inferior parietal cortex integrates time and space during collision judgments. *Neuroimage*, *20*(Suppl. 1), S82–S88.
- Astafiev, S. V., Shulman, G. L., Stanley, C. M., Snyder, A. Z., Van Essen, D. C., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *Journal of Neuroscience*, *23*, 4689–4699.
- Battelli, L., Pascual-Leone, A., & Cavanagh, P. (2007). The “when” pathway of the right parietal lobe. *Trends in Cognitive Sciences*, *11*, 204–210.
- Baumeister, A. A., & Joubert, C. E. (1969). Interactive effects on reaction-time of preparatory interval length and preparatory interval frequency. *Journal of Experimental Psychology*, *82*, 393–395.
- Bueti, D., Bahrami, B., & Walsh, V. (2008). The sensory and association cortex in time perception. *Journal of Cognitive Neuroscience*, *20*, 1–9.
- Bueti, D., Bahrami, B., Walsh, V., & Rees, G. (2010). Encoding of temporal probabilities in the human brain. *Journal of Neuroscience*, *30*, 4343–4352.
- Buonomano, D. V., & Karmarkar, U. R. (2002). How do we tell time? *Neuroscientist*, *8*, 42–51.
- Chawla, D., Rees, G., & Friston, K. J. (1999). The physiological basis of attentional modulation in extrastriate visual areas. *Nature Neuroscience*, *2*, 671–676.
- Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1990). Attentional modulation of neural processing of shape, color, and velocity in humans. *Science*, *248*, 1556–1559.
- Correa, Á., Lupiáñez, J., Milliken, B., & Tudela, P. (2004). Endogenous temporal orienting of attention in detection and discrimination tasks. *Perception & Psychophysics*, *66*, 264–278.
- Correa, Á., Lupiáñez, J., & Tudela, P. (2005). Attentional preparation based on temporal expectancy modulates processing at the perceptual level. *Psychonomic Bulletin & Review*, *12*, 328–334.
- Correa, Á., Lupiáñez, J., & Tudela, P. (2006). The attentional mechanism of temporal orienting: Determinants and attributes. *Experimental Brain Research*, *169*, 58–68.
- Cotti, J., Rohenkohl, G., Stokes, M., Nobre, A. C., & Coull, J. T. (2011). Functionally dissociating temporal and motor components of response preparation in left intraparietal sulcus. *Neuroimage*, *54*, 1221–1230.
- Coull, J., & Nobre, A. (2008). Dissociating explicit timing from temporal expectation with fMRI. *Current Opinion in Neurobiology*, *18*, 137–144.
- Coull, J. T. (2009). Neural substrates of mounting temporal expectation. *PLoS Biology*, *7*, e1000166.
- Coull, J. T., Frith, C. D., Buchel, C., & Nobre, A. C. (2000). Orienting attention in time: Behavioral and neuroanatomical

- distinction between exogenous and endogenous shifts. *Neuropsychologia*, *38*, 808–819.
- Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: The neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *Journal of Neuroscience*, *18*, 7426–7435.
- Coull, J. T., Nobre, A. C., & Frith, C. D. (2001). The noradrenergic alpha2 agonist clonidine modulates behavioural and neuroanatomical correlates of human attentional orienting and alerting. *Cerebral Cortex*, *11*, 73–84.
- Coull, J. T., Vidal, F., Nazarian, B., & Macar, F. (2004). Functional anatomy of the attentional modulation of time estimation. *Science*, *303*, 1506–1508.
- Fabbri-Destro, M., & Rizzolatti, G. (2008). Mirror neurons and mirror systems in monkeys and humans. *Physiology*, *23*, 171–179.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608–2611.
- Ferrandez, A. M., Hugueville, L., Lehericy, S., Poline, J. B., Marsault, C., & Pouthas, V. (2003). Basal ganglia and supplementary motor area subserve duration perception: An fMRI study. *Neuroimage*, *19*, 1532–1544.
- Ghose, G. M., & Maunsell, J. H. (2002). Attentional modulation in visual cortex depends on task timing. *Nature*, *419*, 616–620.
- Granjon, M., Requin, J., Durup, H., & Reynard, G. (1973). Effects of a timing signal on simple reaction time with “non aging” foreperiods. *Journal of Experimental Psychology*, *101*, 139–145.
- Green, D. A., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.
- Griffin, I. C., Miniussi, C., & Nobre, A. C. (2001). Orienting attention in time. *Frontiers in Bioscience*, *6*, D660–D671.
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, *41*, 1409–1422.
- Harrington, D. L., Zimbelman, J. L., Hinton, S. C., & Rao, S. M. (2010). Neural modulation of temporal encoding, maintenance, and decision processes. *Cerebral Cortex*, *20*, 1274–1285.
- Hesse, M. D., Thiel, C. M., Stephan, K. E., & Fink, G. R. (2006). The left parietal cortex and motor intention: An event-related functional magnetic resonance imaging study. *Neuroscience*, *140*, 1209–1221.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, *22*, 751–761.
- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, *23*, 315–341.
- Kastner, S., & Ungerleider, L. G. (2001). The neural basis of biased competition in human visual cortex. *Neuropsychologia*, *39*, 1263–1276.
- Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science*, *293*, 1506–1509.
- Livesey, A. C., Wall, M. B., & Smith, A. T. (2007). Time perception: Manipulation of task difficulty dissociates clock functions from other cognitive demands. *Neuropsychologia*, *45*, 321–331.
- Luppino, G., Murata, A., Govoni, P., & Matelli, M. (1999). Largely segregated parietofrontal connections linking rostral intraparietal cortex (areas AIP and VIP) and the ventral premotor cortex (areas F5 and F4). *Experimental Brain Research*, *128*, 181–187.
- Macar, F., & Vidal, F. (2003). The CNV peak: An index of decision making and temporal memory. *Psychophysiology*, *40*, 950–954.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., et al. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *92*, 8135–8139.
- Martens, S., & Johnson, A. (2005). Timing attention: Cuing target onset interval attenuates the attentional blink. *Memory & Cognition*, *33*, 234–240.
- Mauk, M. D., & Buonomano, D. V. (2004). The neural basis of temporal processing. *Annual Review of Neuroscience*, *27*, 307–340.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford, UK: Oxford University Press.
- Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences*, *6*, 414–417.
- Niemi, P., & Näätänen, R. (1981). Foreperiod and simple reaction time. *Psychological Bulletin*, *89*, 133–162.
- O’Reilly, J. X., Mesulam, M. M., & Nobre, A. C. (2008). The cerebellum predicts the timing of perceptual events. *Journal of Neuroscience*, *28*, 2252–2260.
- Pessoa, L., Kastner, S., & Ungerleider, L. G. (2003). Neuroimaging studies of attention: From modulation of sensory processing to top-down control. *Journal of Neuroscience*, *23*, 3990–3998.
- Pfeuty, M., Ragot, R., & Pouthas, V. (2003). When time is up: CNV time course differentiates the roles of the hemispheres in the discrimination of short tone durations. *Experimental Brain Research*, *151*, 372–379.
- Posner, M. I., Snyder, C., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology*, *109*, 160–174.
- Praamstra, P., Meyer, A. S., Cools, A. R., Horstink, M. W., & Stegeman, D. F. (1996). Movement preparation in Parkinson’s disease. Time course and distribution of movement-related potentials in a movement precueing task. *Brain*, *119*, 1689–1704.
- Renoult, L., Roux, S., & Riehle, A. (2006). Time is a rubberband: Neuronal activity in monkey motor cortex in relation to time estimation. *European Journal of Neuroscience*, *23*, 3098–3108.
- Riehle, A., Grun, S., Diesmann, M., & Aertsen, A. (1997). Spike synchronization and rate modulation differentially involved in motor cortical function. *Science*, *278*, 1950–1953.
- Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron*, *31*, 889–901.
- Roux, S., Coulmance, M., & Riehle, A. (2003). Context-related representation of timing processes in monkey motor cortex. *European Journal of Neuroscience*, *18*, 1011–1016.
- Rushworth, M. F., Ellison, A., & Walsh, V. (2001). Complementary localization and lateralization of orienting and motor attention. *Nature Neuroscience*, *4*, 656–661.
- Rushworth, M. F., Johansen-Berg, H., Gobel, S. M., & Devlin, J. T. (2003). The left parietal and premotor cortices: Motor attention and selection. *Neuroimage*, *20*, S89–S100.
- Rushworth, M. F. S., Nixon, P. D., Renowden, S., Wade, D. T., & Passingham, R. E. (1997). The left parietal cortex and motor attention. *Neuropsychologia*, *35*, 1261–1273.
- Toni, I., Rushworth, M. F. S., & Passingham, R. E. (2001). Neural correlates of visuomotor associations. Spatial rules compared with arbitrary rules. *Experimental Brain Research*, *141*, 359–369.

- Triviño, M., Correa, A., Arnedo, M., & Lupiáñez, J. (2010). Temporal orienting deficit after prefrontal damage. *Brain*, *133*, 1173–1185.
- Vallesi, A., McIntosh, A. R., Shallice, T., & Stuss, D. T. (2009). When time shapes behavior: fMRI evidence of brain correlates of temporal monitoring. *Journal of Cognitive Neuroscience*, *21*, 1116–1126.
- Vallesi, A., Shallice, T., & Walsh, V. (2007). Role of the prefrontal cortex in the foreperiod effect: TMS evidence for dual mechanisms in temporal preparation. *Cerebral Cortex*, *17*, 466–474.
- VanRullen, R., Pascual-Leone, A., & Battelli, L. (2008). The continuous Wagon wheel illusion and the “when” pathway of the right parietal lobe: A repetitive transcranial magnetic stimulation study. *PLoS One*, *3*, e2911.
- Wiener, M., Turkeltaub, P., & Coslett, H. B. (2010a). The image of time: A voxel-wise meta analysis. *Neuroimage*, *49*, 1728–1740.
- Wiener, M., Turkeltaub, P., & Coslett, H. B. (2010b). Implicit timing activates the left inferior parietal cortex. *Neuropsychologia*, *48*, 3967–3971.
- Woodrow, H. (1914). The measurement of attention. *Psychological Monographs*, *17*, 1–158.
- Zahn, T. P., & Rosenthal, D. (1966). Simple reaction time as a function of the relative frequency of the preparatory interval. *Journal of Experimental Psychology*, *72*, 15–19.

Copyright of Journal of Cognitive Neuroscience is the property of MIT Press and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.