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Original Article

ORIGINAL ARTICLE

Dorsal Anterior Cingulate, Medial Superior Frontal Cortex, and Anterior Insula Show Performance Reporting-Related Late Task Control Signals

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Abstract

The cingulo-opercular network (including the dorsal anterior cingulate and bilateral anterior insula) shows 3 distinct task-control signals across a wide variety of tasks, including trial-related signals that appear to come online at or near the end of the trial. Previous work suggests that there are separable responses in this network for errors and ambiguity, implicating multiple types of processing units within these regions. Using a unique paradigm, we directly show that these separable responses withhold activity to the end of the trial, in the service of reporting performance back into the task set. Participants performed a slow reveal task where images were presented behind a black mask which was gradually degraded, and they pressed a button when they could recognize the object that was being revealed. A behavioral pilot was used to identify ambiguous stimuli. We found interactive effects of accuracy and ambiguity, which suggests that these regions are computing and utilizing information, at one time, about both types of performance indices. Importantly, we showed a relationship between cingulo-opercular activity and behavioral performance, suggesting a role for these regions in performance reporting, per se. We discuss these results in the context of task control.

Key words: ambiguity, error, functional networks, performance reporting, task control

Introduction

Extant work using mixed block/event-related designs, which allow for the modeling of both sustained and transient signals during a task, have demonstrated that a set of regions in the cingulo-opercular network (including the dorsal anterior cingulate/medial superior frontal cortex; dACC/msFC, and bilateral anterior insula/frontal operculum; aI/fO) show 3 distinct task-control signals across a wide variety of tasks. Specifically, they show: (1) a transient start signal at the beginning of a task block, which may include signals related to the loading of task parameters, (2) a sustained signal across an entire task block, presumably related to task maintenance, and (3) trial-related signals, which we associate with performance reporting (Dosenbach et al. 2006, 2007). In particular, these latter trial-related signals have been found in response to errors (Dosenbach et al. 2006; Neta et al. 2014; Neta et al. 2015), conflict (Carter et al. 1998; Botvinick et al. 1999; MacLeod and MacDonald 2000; Botvinick et al. 2001), particularly when the task requires a response relevant to that conflict (Milham et al. 2001), ambiguity (Thompson-Schill et al. 1997; Sterzer et al. 2002; Neta et al. 2013, 2014), monitoring of

performance outcomes (Monchi et al. 2001; Wessel et al. 2012), cognitive set shifting (Konishi et al. 1998), and they show activity that is modulated by reaction time (Grinband et al. 2011). The combination of these processes suggest that these regions are involved in controlling goal-directed behavior including the stable maintenance of task set (see Dosenbach et al. 2008 for a review).

To focus only on the third type of task-control signal, another line of research using an extended trial paradigm has shown that these transient signals in the cingulo-opercular network come online at or near the end of the trial, further suggesting that these responses serve as performance reporting signals (Ploran et al. 2007; Ploran et al. 2011). Specifically, in a slow reveal design where images are presented behind a black mask which was gradually degraded, participants were required to press a button when they could recognize the object that was being revealed. They found that activity in the cingulo-opercular regions stayed low until the moment of recognition, coming online only at or near the end of the trial. This was taken as initial evidence that these regions might be important for performance reporting, per se. Recently, we have gone on to demonstrate that similar cingulo-opercular regions are, at one time, able to report multiple task-control signals (errors, ambiguity, reaction time), which we suggested may be in the service of performance feedback, or reporting performance back into the task set in order to improve behavior on subsequent trials (Neta et al. 2014). Importantly, we suggest that the cingulo-opercular regions are not necessarily part of a closed feedback loop, but rather they appear to report the response outcomes (e.g., whether the response was correct or not), for a number of potential signals at one time (errors, ambiguity, etc.). However, the experimental design in this work did not allow us to model the stages of processing within a trial where decisions about ambiguity are required. As such, the primary goal of the present study was to modify the slow reveal design used by Ploran et al. (2007) to include items that are ambiguous. We predict that the regions previously identified as showing separable trial-related reporting signals (Neta et al. 2014) withhold activity to the end of the trial. This direct analysis of previously identified regions would bolster our argument for their broad role in performance reporting, per se.

Finally, in our previous work, we asked participants to categorize ambiguous stimuli in several different tasks, but in each of these tasks, it was not possible to make an incorrect judgment. For example, in earlier work, we asked participants to make a valence judgment about ambiguously valenced emotional stimuli (e.g., surprised facial expressions can be interpreted as either positive or negative, so either rating was considered a correct response; Neta et al. 2013). Subsequently, we asked participants to make semantic abstract/concrete judgments about ambiguous words (e.g., the word "SAFE" could be considered abstract—as in the absence of danger—or concrete—as in a place to store valuables), and also phonological rhyming judgments about word pairs (e.g., the heteronym BASS might rhyme with GRACE, depending on how it is pronounced; Neta et al. 2014). Taken together, this work did not allow us to compare accuracy and ambiguity effects within a trial because the ambiguous items were always rated correctly, regardless of the response made. In the present work, we used a type of perceptual ambiguity, whereby visual objects were slowly revealed, and ambiguity arises because the incomplete visual information points to multiple competing alternatives (i.e., the items share visual attributes with many other objects, (e.g., toothbrush, pen, paintbrush, rolling pin), whereas clear stimuli have a somewhat unique set of attributes (e.g., butterfly). Indeed, ambiguity has been described as a co-activation and/or selection among competing response options (Thompson-Schill et al. 1997; Sterzer et al. 2002; see Grinband et al. 2011). However, by the end of the trial, at which point the object is fully revealed, the ambiguity is resolved and the correct identification is made available. As such, this paradigm allows us to examine effects of accuracy and ambiguity within a trial. We predict that there will be interactive effects of accuracy and ambiguity in the cingulo-opercular regions, particularly coming online at or near the end of the trial, consistent with previous work that shows that these regions can, at one time, compute and utilize information from both of these signals. In other words, we predict a pattern whereby there is greater activity for ambiguous than clear trials, more so for error than correct trials.

Taken together, we suggest that the cingulo-opercular regions are reporting response outcomes. This report is multifarious: the regions report on a variety of performance-related signals including but "not limited to" accuracy, ambiguity, and reaction time. Importantly, these regions seem to report, as opposed to predict (as in the PRO model), response outcomes given that the onset of the signals come online late in the trial, when the participant makes a response. Although we focus in the present work only on the control signals that take place on a trialwise basis, this control system also shows a variety of types of control-related signals (task initiation and maintenance). The trialwise signals discussed here represent only one piece of the role of this network in task control; one that occurs every time a trial is completed, and they appear to report on a variety of performance-related signals that occurred during that trial. While we focus here only on performance signals related to accuracy and ambiguity/conflict, it stands to reason that many other types of signals (e.g., reward) might also elicit similar signals. This reporting of information related to the completed trial is useful for future updating and implementing this information on subsequent trials.

One goal of the present work is to determine if these late performance-related control signals that have been previously shown in the context of errors (Wheeler et al. 2008) are also found for ambiguity. In other words, we predict that these regions are not part of the decision-making process (e.g., they are not resolving ambiguity), but rather, they make a note of performance upon completion of an ambiguous trial, rather than beginning to ramp up earlier in the trial, during the competition of alternative response options.

Materials and Methods

Stimuli

The pictures were 251 grayscale images (Rossion and Pourtois 2004) reformatted into a standard 284 × 284 pixel image with a white background. The displayed images subtended an average of 10.3° of the visual field and were presented against a black background. One image was reserved for a practice trial, in order for participants to get acquainted with the task; 10 lists of 25 pictures were selected out of the remaining 250 pictures for task presentation.

Behavioral Pilot

In a behavioral pilot, we recruited a total of 19 participants (11 female). Each participant viewed 274 images in the slow reveal paradigm (see Task below functional magnetic resonance imaging [fMRI] Experiment) in one of 2 versions (9 participants saw version 1, 10 saw version 2). Images were presented in a random order, and these 2 versions simply represented 2 randomized pre-set orders of presentation. From these data, we

excluded 24 images that had a very low response rate (12 or fewer of the 19 participants made any response indicating they knew what the image was depicting). Of the remaining 250 items, we identified 108 ambiguous items based on accuracy, where the average accuracy was 80% or less across participants. The remaining 142 items were classified as clear (unambiguous), with an accuracy of over 80% across participants, and a response rate of 13 or more participants. In sum, ambiguous items were characterized as those items that are more difficult to recognize with incomplete visual information, and this difficulty likely arises because the incomplete visual information points to multiple competing alternatives (i.e., the items share visual attributes with many other objects, e.g., toothbrush, pen, paintbrush, rolling pin), whereas clear stimuli have a somewhat unique set of attributes (e.g., butterfly, see Fig. 1).

Participants

Twenty-eight healthy participants (right-handed, without neurological disease and with normal/corrected vision, 15 female, ages 21–30 years, mean age = 25.7) volunteered. None were aware of the purpose of the experiment, and all were compensated for their participation through monetary payment. Written informed consent was obtained from each participant before the session. All procedures were approved by the Washington University Committee for the Protection of Human Subjects. One participant was excluded because she had prior experience with the stimuli. The final sample included 27 participants (14 females).

fMRI Experiment

Testing consisted of 10 runs of a perceptual recognition task using picture stimuli, with 25 trials per run, where 10 or 11 trials

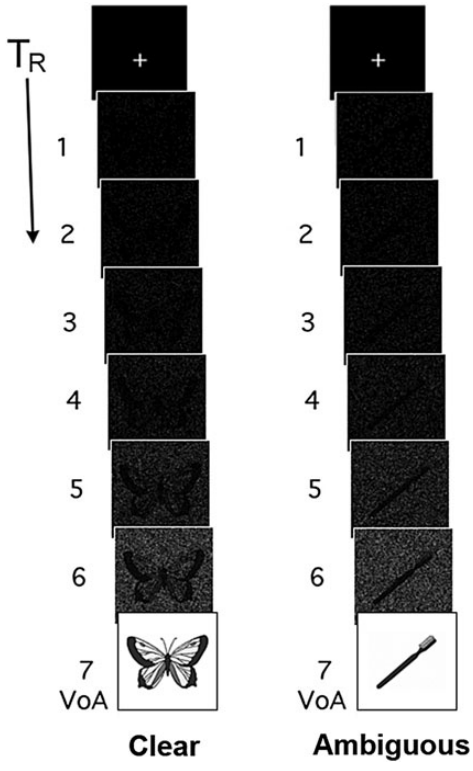

Figure 1. This is a depiction of the slow reveal design, where we show one example for a clear stimulus, and one for an ambiguous stimulus.

were previously identified as ambiguous (see Pilot), and 14 or 15 were clear. There were 2 versions of the experiment, and half of the participants completed each version. Because some runs contained 10 ambiguous images, and other runs contained 11, in these 2 versions, we counterbalanced the order of these different of runs, and randomized the order of the conditions and images within each run. Before beginning the experiment, subjects were given one practice trial in order to get acquainted with the task. The task was the same as the one used in previous work (see, Ploran et al. 2007), where, in each trial, stimulus revelation occurred over 7 discrete steps, each corresponding with acquisition of a whole-brain image (Fig. 1). The revelation steps occurred every 2 s without within-trial jitter. Between-trial jitter of 2, 4, or 6 s (mean intertrial interval [ITI] = 4 s) was included in both experiments to allow event-related analysis of individual trials.

At trial onset, pictures were covered by a black mask. The mask partially dissolved at each successive 2-s interval (i.e., revelation step) until pictures were completely revealed (Fig. 1). Participants were instructed to press a button when they could identify the picture with a reasonable degree of confidence (time of recognition, T_R). Participants were encouraged to respond as soon as they had a relatively high level of confidence in the identity of the object in the picture, and they were specifically encouraged to respond before the items were fully revealed. When stimuli were fully revealed (VoA), participants pressed the same button again only if their earlier recognition had been correct. As in previous work, we used gradual stimulus revelation over other unmasking procedures (e.g., mask degradation remains constant but areas revealed change from step to step) because we could readily map the quantity of stimulus input onto neural activity as a linear increase across the trial (Carlson et al. 2006). To help factor out basic lateralized motor signals in group analyses, response hand was counterbalanced across participants (Thielscher and Pessoa 2007). Psyscope X was used for stimulus presentation and data collection (Cohen et al. 1993) (http://psy.ck.sissa.it).

Imaging Acquisition

Images were acquired on a Siemens 3 T TIM Trio scanner (Erlanger, Germany) with a 12-channel Siemens Matrix head coil. A T_1-weighted MPRAGE structural image was obtained (slice time echo = 3.08 ms, time repetition [TR] = 2.4 s, time to inversion [TI] = 1000 ms, flip angle = 8°, 176 slices, 1 × 1 × 1 mm voxels). All functional runs were acquired parallel to the anterior–posterior commissure plane using a blood oxygen level-dependent (BOLD) contrast-sensitive asymmetric spin-echo echo-planar sequence (TE = 27 ms; volume TR = 2 s, flip angle = 90°, in-plane resolution = 4 × 4 mm). Whole-brain coverage was obtained with 32 contiguous interleaved 4 mm axial slices. An auto-align pulse sequence protocol provided in the Siemens software was used to align the acquisition slices to the anterior and posterior commissure (AC–PC) plane and centered on the brain. A T_2-weighted turbo spin-echo structural image (TE = 84 ms, TR = 6.8 s, 32 slices with 1 × 1×4 mm voxels) was also obtained in the same anatomical plane as the BOLD images to improve alignment to the atlas.

Each subject was fitted with a thermoplastic mask fastened to the head coil using custom-made clamps to help stabilize head position. Additionally, the first 4 frames of the BOLD time series were skipped to assure steady-state magnetization.

Visual stimuli were generated on an Apple iMac with PsyScope X and projected onto a screen positioned at the head of

the magnet bore using a Sharp PG-M20X digital multimedia projector via a mirror attached to the head coil. Earplugs dampened scanner noise. Responses were made using a fiber optic button stick connected to the computer via an interface unit (Current Designs, Philadelphia, PA).

Analyses

Behavioral Analyses

In order to determine when in the course of the trial participants were able to recognize each object, we calculated, for each participant, the rate of responses for each T_R, and by condition. For example, let's assume that subject 1 correctly recognized a total of 81 ambiguous items, and that they indicated this recognition judgment (i.e., they made their response) during T_R6 on 14 of those 81 trials. Moreover, on all 14 of those 81 trials, they also indicated that their recognition judgment was correct, so they were able to accurately identify these ambiguous items in T_R6. In this case, this subject will have a value of 14/81 = 0.172, or 17.2% for ambiguous correct trials in T_R6. We then calculated this response rate for each T_R by condition (ambiguous correct, ambiguous error, clear correct, clear error). This dependent variable allowed us to take into account the number of trials on which subjects were able to correctly (or incorrectly) recognize the ambiguous and clear items, and to see the distribution of these responses across the 6 T_Rs. Then, we ran a repeated-measures analysis of variance (ANOVA) on accuracy (correct, error) × ambiguity (ambiguous, clear) × T_R (1–6).

Imaging Analyses.*Preprocessing*. Initial data processing to remove noise and artifacts was carried out using a series of automated steps, including (1) temporal realignment using sinc interpolation of all slices to the temporal midpoint of the first slice, accounting for differences in the acquisition time of each individual slice, (2) correction for movement within and across BOLD runs using a rigid-body rotation and translation algorithm (Snyder 1996), and (3) whole-brain intensity normalization for each functional run by multiplying the intensity value of all of the voxels by a single factor to achieve a modal value of 1000 across all of the image voxels to allow comparisons across subjects (Ojemann et al. 1997). Functional data were then resampled into 2-mm isotropic voxels and transformed into stereotaxic atlas space (Talairach and Tournoux 1988). Atlas registration involved aligning each subject's T_1-weighted image to a custom atlas-transformed (Lancaster et al. 1995) target T_1-weighted template using a series of affine transforms (Michelon et al. 2003; Fox et al. 2005).

General linear models. Preprocessed data were analyzed at the voxel level using a general linear model (GLM) approach (Friston et al. 1994; Miezin et al. 2000). Details of this procedure are described by Ollinger et al. (2001). Estimates of the time course of effects were derived from the model for each response category by coding 14 time points as a set of gamma functions immediately after onset of the coded event (Ollinger et al. 2001). In other words, the shape of the BOLD response was not included in the GLM but rather estimated from 14 time points included in the design matrix for the GLM (Miezin et al. 2000). Over each run, a trend term accounted for linear changes in signal, and a constant term modeled the baseline signal. Event-related effects are described in terms of percentage signal change, defined as signal magnitude divided by a constant term. Again, this approach makes no assumptions about the shape of the BOLD response but does assume that all events included in a category (e.g., accurate T_R6) are associated with the same BOLD response (Friston et al. 1994; Worsley et al. 1995; Josephs et al. 1997; Zarahn et al. 1997a, 1997b; Miezin et al. 2000; Ollinger et al. 2001; Wheeler et al. 2006). Thus, we could extract time-courses without placing constraints on their shape. Image processing and analyses were performed using in-house software written in IDL (Research Systems, Boulder, CO).

In total, we computed 2 different GLMs. For our primary goal, we examined the time courses by T_R across all trial conditions, in order to determine if our a priori regions of interest in cingulo-opercular regions (see Neta et al. 2014) showed activity that remains low until the moment of recognition. For this analysis, the 5 events we modeled corresponded to the T_R 2–6 (excluding the T_R1 because most participants did not make any responses during this frame). In order to include as many subjects as possible, we collapsed across the trial conditions for this analysis. The task-related transient parameters were taken to a second level for random-effect analysis using f tests. A significant main effect of time (ANOVA) indicated that the hemodynamic response was different from flat across the 7 T_Rs. One subject did not make any responses in the last T_R, so the final sample for these analyses had 26 subjects (14 females).

For our second GLM, we collapsed T_R into 2 bins: T_R3–4, and T_R5–6, and the 8 events we modeled were the ambiguous correct, ambiguous error, clear correct and clear error trials for each bin (the second button press at the VoA was not modeled in either GLM). Importantly, at the time of the first button press, the subject does not yet know that the percept was wrong, but many error-related signals can happen in the absence of explicit feedback about the error or clear awareness on the part of the subject (Nieuwenhuis et al. 2001). As such, error-related activity can be modeled based on the first button press. Also, because of a low rate of response during the first 2 T_Rs, those trials were coded as a condition of no interest, along with errors of omission. As with the first GLM, the task-related transient parameters were taken to a second level for random-effect analysis using f tests. Two subjects did not make any errors on clear trials in at least one of the 2 bins, so the final sample for these analyses had 25 subjects (13 females). For both GLMs, individual subject data were transformed into the stereotactic space of Talairach and Tournoux (1988).

Regions of interest definition. We focused our analyses on 3 control regions that we have shown respond to errors and ambiguity (Neta et al. 2014). Specifically, we constructed 3 regions of interest (ROIs) derived from our previous coordinates in dorsal anterior cingulate/medial superior frontal cortex (dACC/msFC) (−2, 19, 49) and bilateral aI/fO (right aI/fO: 33, 25, −1; left aI/fO: −33, 24, 1). Functional ROI volumes were defined as 10-mm diameter spheres at these coordinates. We submitted these ROIs to further testing in a repeated-measures ANOVA of T_R (2, 3, 4, 5, 6) × time-course (14 frames).

We then submitted these ROIs to further testing in more focused repeated-measures ANOVAs which included independent variables for accuracy (error, correct) and ambiguity (ambiguous, clear), and only a subset of the time-course data. Specifically, using a previously published examination of error-related activity as a model (Wheeler et al. 2008), we ran an accuracy (correct, error) × ambiguity (ambiguous, clear) × time-course (3 levels of time that included the 3 frames after the stimulus has been fully revealed, and the ambiguity had been necessarily resolved; timepoints 9–11).

Subsequently, we tested the effect of timing by including epoch (pre-recognition and post-recognition). In other words,

we ran an accuracy × ambiguity × epoch (pre, post) repeated-measures ANOVA. For the pre-recognition epoch, we included timepoints 4–6, just prior to recognition decisions occurring in the last bin (T_Rs 5/6). Due to averaging, it also necessarily encompasses 2 sec of post-recognition time at frame 6. However, with an assumed 2 to 3-sec lag in the onset of the BOLD response, and a 4 to 6-sec lag in the time-to-peak (Miezin et al. 2000), activity in this time window should be almost exclusively related to processing prior to recognition. For the post-recognition epoch, we included timepoints 9–11, after the stimulus was fully revealed.

Finally, we tested effects of region by including region as a between subjects variable in a final repeated-measures ANOVA.

Results

Behavioral

Participants Wait Longer to Respond to Ambiguous Than Clear Trials

We ran a repeated-measures ANOVA on accuracy (correct, error) × ambiguity (ambiguous, clear) × T_R (1–6) using the percentage of trials for each condition (see Materials and Methods). We found a significant ambiguity × T_R interaction ($F_{5,22} = 21.27$, $P < 0.001$), where there were more responses for clear than ambiguous trials in T_Rs 2 ($P < 0.001$) and 3 ($P = 0.001$), but more responses for ambiguous than clear trials in T_Rs 5 ($P = 0.07$) and 6 ($P < 0.001$; Fig. 2). In other words, participants were identifying the ambiguous items later in the trial (after more information was revealed) compared with clear items, suggesting that our identification of these items as ambiguous was accurate (see means and standard errors of response distribution in Table 1).

There was also a significant accuracy × ambiguity × T_R interaction ($F_{5,22} = 3.34$, $P = 0.022$), such that the above effect was significant for correct trials in T_Rs 1–3 (clear > ambiguous, P's ≤ 0.003), and T_Rs 5 and 6 (ambiguous > clear, $P < 0.001$), and for error trials in T_R 3 (clear > ambiguous, $P = 0.023$) and 6 (ambiguous > clear, $P < 0.001$).

Imaging

Three a Priori Cingulo-opercular Regions Show Activity Stays low Until the Moment of Recognition

In order to determine whether or not our previously defined control regions come online at the end of the trial, likely in the service of a performance reporting mechanism, we made 3 ROIs using our previous coordinates in dACC/msFC (−2, 19, 49) and bilateral aI/fO (right aI/fO: 33, 25, −1; left aI/fO: −33, 24, 1). We then submitted these ROIs to further testing in a repeated-measures ANOVA of T_R (2, 3, 4, 5, 6) × timecourse (14 frames), and found a significant main effect of T_R in dACC ($F_{4,22} = 2.92$, $P < 0.05$), left aI/fO ($F_{4,22} = 2.89$, $P < 0.05$), and right aI/fO ($F_{4,22} = 5.44$, $P = 0.003$). As expected, activity in all 3 regions stays low until the moment of recognition (Fig. 3).

Regions Show Late Effects for Accuracy and Ambiguity

To examine accuracy- and ambiguity-dependent differences in these regions, we ran a repeated-measures ANOVA on a subset of the time-course data, focusing on the period of time after the stimulus has been fully revealed (i.e., after the moment of recognition, when these effects are expected to come online). We focused only on data from the last time bin (T_Rs 5 and 6), which gave us the greatest number of trials and occurred just before the stimulus was revealed. There were 2 levels of accuracy (correct, error), 2 levels of ambiguity (ambiguous, clear), and 3 levels of time (timepoints 9–11 for the post-recognition epoch of interest). We found a significant main effect of ambiguity ($F_{1,2} = 46.68$, $P < 0.03$), where activity was greater for ambiguous than clear trials, and a significant main effect of accuracy ($F_{1,2} = 53.02$, $P < 0.02$), where activity was greater for error than correct trials. There was also a trend for a significant ambiguity × accuracy interaction ($F_{1,2} = 14.75$, $P = 0.06$), such that there was greater activity for ambiguous than clear trials, more so for error than correct trials (blue shaded area; Fig. 4).

To examine the effect of timing, we included epoch (timepoints 4–6 immediately prior to recognition decisions occurring

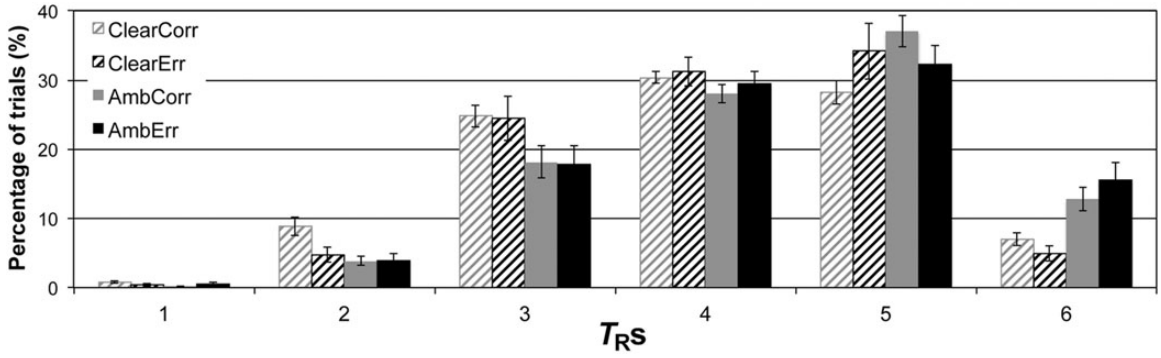

Figure 2. Behavioral data. The y-axis shows the percentage of trials from each condition. Each line represents trials on which the participant made a recognition judgment during T_R 2, 3, 4, 5, or 6. There were more responses for clear than ambiguous trials in early T_Rs (2 and 3), but more responses for ambiguous than clear trials in later T_Rs (5 and 6). In other words, participants were identifying the ambiguous items later in the trial (after more information was revealed) compared with clear items.

Table 1 Mean and standard error of response distribution by T_R

	T_R 1	T_R 2	T_R 3	T_R 4	T_R 5	T_R 6
Clear correct	1 ± 0.2	10.2 ± 1.5	29.4 ± 1.6	36.8 ± 1.5	34.0 ± 2.3	8.5 ± 1.2
Clear error	0.1 ± 0.06	1.4 ± 0.4	5.4 ± 1.0	6.8 ± 1.1	5.7 ± 0.7	0.8 ± 0.2
Ambiguous correct	0.1 ± 0.06	2.5 ± 0.4	12.2 ± 1.2	20.3 ± 1.0	27.9 ± 2.1	10.0 ± 1.4
Ambiguous error	0.2 ± 0.09	1.5 ± 0.5	6.6 ± 1.4	10.0 ± 1.4	9.5 ± 1.0	4.0 ± 0.6

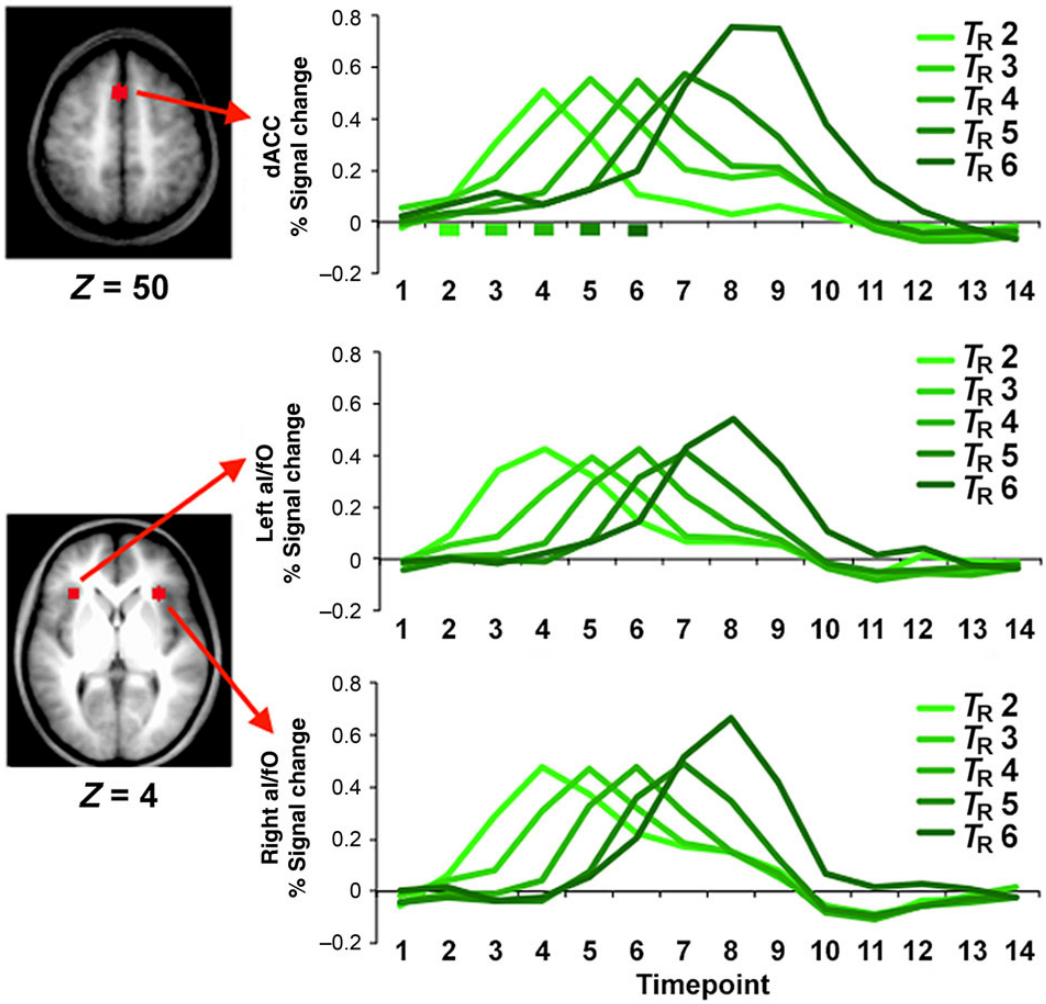

Figure 3. We found that activity in the cingulo-opercular regions comes online at or near the end of the trial, suggesting a role for these regions in performance reporting. Slices on the left represent anatomical depictions of the ROIs.

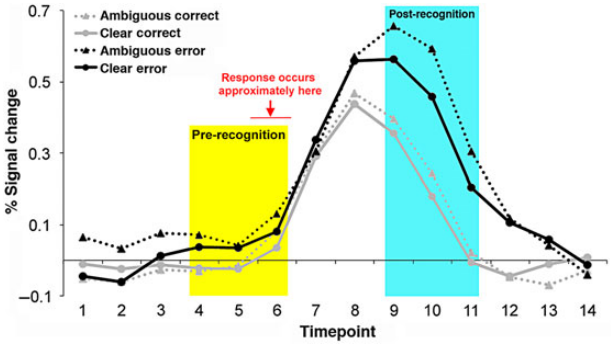

Figure 4. Cingulo-opercular regions withhold their activity until the moment of recognition. They also show accuracy-related effects both in the pre-recognition epoch (yellow), and post-recognition epoch (blue). There are ambiguity-related effects post-recognition, and a trend for an effect pre-recognition. Interestingly, there are interactive effects of ambiguity and accuracy only post-recognition, where there is greater activity for ambiguous than clear trials, more so for error than correct trials. Time courses are calculated based on signal averaged across the 3 regions of interest.

in this last bin (T_Rs 5/6), and timepoints 9–11 after the stimulus was fully revealed) as a repeated factor. There was a significant main effect of epoch ($F_{1,2} = 36.81$, $P < 0.03$), where activity was greater post-recognition than pre-recognition, as expected. There was also a significant ambiguity × epoch interaction ($F_{1,2} = 9.23$, $P < 0.02$), such that ambiguous > clear trials post-recognition (blue shaded area in Fig. 4; $P < 0.03$), but there was only a trend for such an effect pre-recognition (yellow shaded area in Fig. 4; $P = 0.099$). There was also a significant accuracy × epoch interaction ($F_{1,2} = 38.80$, $P < 0.03$), such that error > correct activity both pre- and post-recognition (P's < 0.02). Finally, there was a trend for a significant ambiguity × accuracy × epoch interaction ($F_{1,2} = 12.01$, $P < 0.08$), such that there was ambiguous > clear activity more so for error than correct trials, but this pattern was only significant post-recognition (P's < 0.04). Pre-recognition, there was a trend for ambiguous > clear only for "correct" trials ($P < 0.09$). This pattern of activity is strikingly similar to the activity in regions previously defined as moment-of-recognition regions (see Supplementary Fig. 1). For a similar analysis and figure examining T_Rs 3/4, see Supplementary Material and Figure 2.

To determine whether there was any difference between the regions, we included region as a factor. There was a significant main effect of region ($F_{2,72} = 4.57$, $P < 0.02$), where activity was greater in dACC than bilateral aI/fO (P's < 0.01), but there was no significant difference between the insula regions ($P > 0.8$). Importantly, there were no significant interactions between region and ambiguity or accuracy (P's > 0.1).

Late Effects Appear to be Related to Performance Reporting

To test whether these late effects were related to performance reporting, per se, we compared activity in these regions to behavioral performance. First, we ran an accuracy (correct, error) × ambiguity (ambiguous, clear) repeated-measures ANOVA on performance for the subsequent trial (i.e., dependent variable was accuracy on trials following an error, an ambiguous item, etc.). There were significant main effects of accuracy ($F_{1,26} = 9.27$, $P = 0.005$) and ambiguity ($F_{1,26} = 5.21$, $P = 0.03$), such that performance was improved following errors and ambiguity. There was also a trend for a significant accuracy × ambiguity interaction ($F_{1,26} = 3.45$, $P = 0.074$). Post hoc tests revealed that there was a significant difference between error and correct trials, but only for ambiguous trials ($P < 0.001$; clear trials $P > 0.3$), and there was a significant difference between ambiguous and clear trials, but only for errors ($P = 0.02$; clear trials $P > 0.9$). For further analyses to test the specificity of these effects, see Supplementary Material. This suggests that the putative reporting response during errors and ambiguous trials may result in improved task performance.

Next, we examined individual differences in brain activity across these 3 regions of interest, and compared that with performance. To do this, we averaged the peak response in each region (frames 8–10) for each condition (ambiguous correct, clear correct, ambiguous error, and clear error), and then averaged across the 3 ROIs, to come up with a value representing the level of activity for each subject. We found that activity for clear error trials correlated with accuracy on trials following clear errors ($r = 0.62$, $P < 0.005$; Fig. 5A), such that individuals showing the greatest activity showed the greatest performance on the subsequent trial. This activity for clear errors was also correlated with overall performance ($r = -0.53$, $P < 0.01$; Fig. 5B), such that individuals showing the greatest activity also made the least number of total errors.

There was a similar effect for ambiguity; there was a significant correlation between activity for ambiguous correct trials and accuracy on trials following ambiguous correct trials ($r = 0.48$, $P < 0.02$; Fig. 5C), such that individuals showing the greatest activity showed that greatest performance on the subsequent trial. And this effect was significant also for ambiguous error trials ($r = 0.42$, $P < 0.04$; Fig. 5D), where individuals showing the greatest activity for ambiguous errors showed that greatest performance on the subsequent trial. Importantly, there were no significant correlations between activity during clear correct trials and performance (p's > 0.1). To further test the specificity of these individual differences effects, we ran a few follow-up analyses (see Supplementary Material).

Discussion

The present experiment uses a modified version of a slow reveal design, which allows for the modeling of the onset of responses within a trial, in order to separate responses that come online early (e.g., evidence accumulation) from those that come online

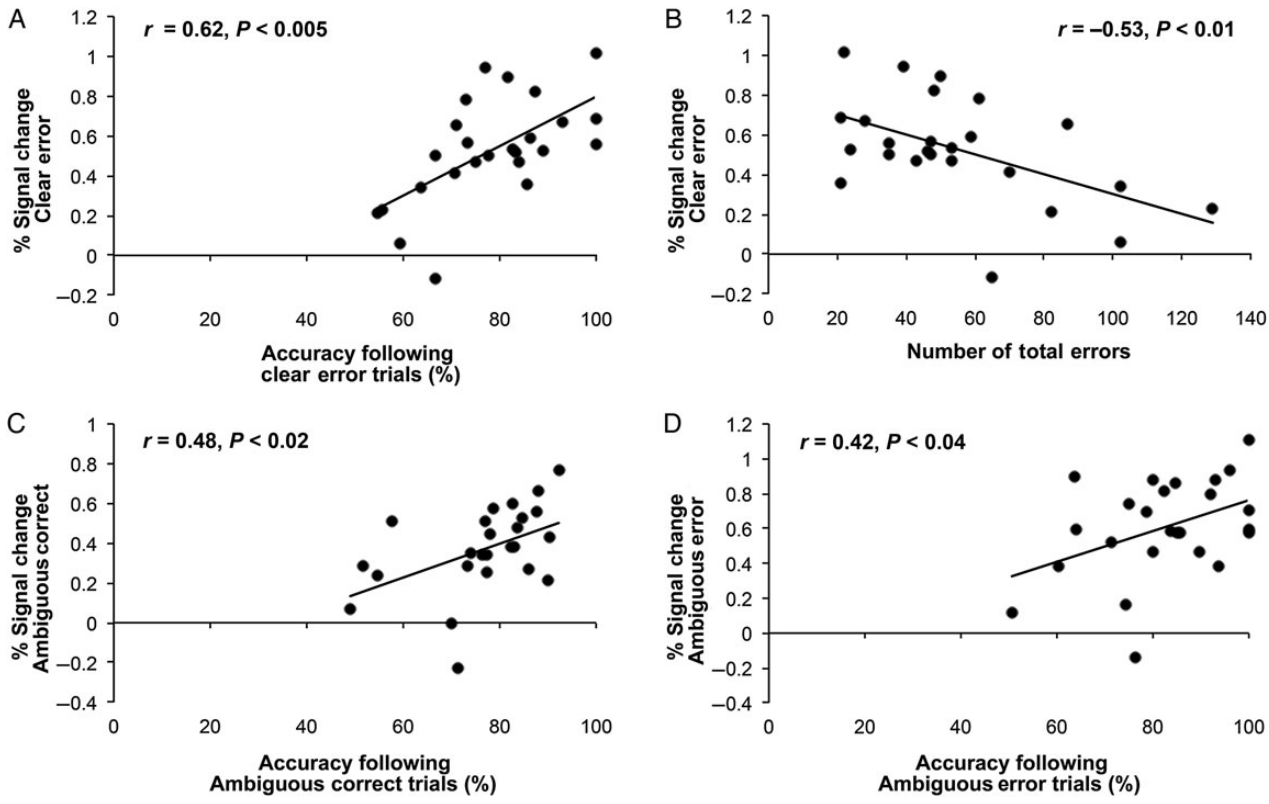

Figure 5. Cingulo-opercular activity is important for performance reporting. This is based on an averaged peak response in each region (frames 8–10) for each condition (ambiguous correct, clear correct, ambiguous error, and clear error), then averaged across the 3 ROIs, to come up with a value representing the level of activity for each subject. (*A*) Activity for clear error trials correlated with accuracy on trials following clear errors ($r = 0.62$, $P < 0.005$), such that individuals showing the greatest activity showed that greatest performance on the subsequent trial. (*B*) This activity for clear errors was also correlated with overall performance ($r = -0.53$, $P < 0.01$), such that individuals showing the greatest activity also made the least number of total errors. (*C*) There was a similar effect for ambiguity; activity for ambiguous correct trials was correlated with accuracy on subsequent trials ($r = 0.48$, $P < 0.02$), such that individuals showing the greatest activity showed that greatest performance on the subsequent trial. (*D*) This effect was significant also for ambiguous error trials ($r = 0.42$, $P < 0.04$).

late (e.g., moment of recognition) during an object recognition task. Specifically, we have modified the task by adding a manipulation of stimulus ambiguity, where some items were more difficult than others to identify based on little visual information because they share visual properties with many other objects, see Methods and Figure 1.

The goal of this report is 2-fold: First, we replicated previous work showing that error-related activity comes online at or near the end of the trial (Ploran et al. 2007; Ploran et al. 2011), and extended this to include late ambiguity-related activity in a perceptual decision-making task. Second, we asked whether ambiguity and accuracy processing show interactive effects that come online as a late performance reporting signal. Importantly, error-related activity can come online in the absence of explicit feedback or any awareness on the part of the subject (Nieuwenhuis et al. 2001). So the error-related response need not wait until the image is fully revealed at the end of the trial; it could come online immediately after a participant makes an erroneous response.

Separable Error and Ambiguity Signals Related to Performance Reporting

We have recently demonstrated that a set of regions in the cingulo-opercular network, including the dorsal anterior cingulate extending into the medial superior frontal cortex, and the bilateral anterior insula extending into the frontal operculum, show separable responses to errors, ambiguity, and reaction time (Neta et al. 2014). Based on previous work (Ploran et al. 2007), we suggested that these signals likely come online at or near the end of the trial, providing further evidence that these signals might be in the service of performance reporting to a task-control system. Here, we have shown that, across items that are both ambiguous and clear, and both correctly and incorrectly recognized, the cingulo-opercular regions withhold activity to the time of decision. This fits much more cleanly with a performance reporting explanation than other components of task control (e.g., online or adaptive monitoring). In our original conception of the 2 control networks (cingulo-opercular and fronto-parietal), we suggested that a major difference was whether the control was applied at a task level or had ongoing adaptive responsibility (Dosenbach et al. 2006, 2007). The cingulo-opercular network, with its sustained signals, was thought to be more closely related to overall task control, and the fronto-parietal in the more adaptive role. Further distinction can be found with regard to the signals that are found in each network: Ploran et al. (2007) reported that the fronto-parietal regions were more related to evidence accumulation, where the activity in these regions comes online early and slowly ramps up as greater information about the stimulus is revealed. In contrast, activity in the cingulo-opercular regions stays low while evidence is accumulated and only comes online after the decision is made (for a replication of these findings in the present data, see Supplementary Fig. 1). We believe the late responses in the cingulo-opercular network fit with a reporting of the events of the trial (e.g., ambiguity) and its response outcomes because these regions are not active until after a decision is made and, only then, do they come into the picture. The fronto-parietal regions, in contrast, seem to be active during the problem-solving stage of the process.

Furthermore, we replicated previous work showing that this late response in cingulo-opercular regions is greater on error than correct trials (Wheeler et al. 2008). As an extension of these findings, we found a similar effect for ambiguity, whereby there was ambiguous > clear activity in these regions that comes online only after the moment of recognition. This is consistent with work showing that the regions in the cingulo-opercular network (i.e., dorsal anterior cingulate/medial superior frontal cortex, bilateral anterior insula/frontal operculum), show responses to errors (see Dosenbach et al. 2006; Neta et al. 2015) and ambiguity (Neta et al. 2013), and, more specifically, that they show separable responses to errors and ambiguity in the service of task control (Neta et al. 2014). One might have predicted that ambiguity would not work the same way as accuracy, that activity might begin to ramp up in these regions earlier in the trial, during the competition of alternative response options, but ambiguity appears to work the same as errors. Taken together, we suggest that these cingulo-opercular regions appear to report on ambiguity and accuracy (and perhaps a variety of other performance-related signals such as costs and benefits) in a similar manner, but only at a relatively specific time (after a response has been made and the task—as far as that trial is concerned—is complete). These multiple performance reporting signals are likely useful in response to situations of uncertainty (ambiguity) and error, in order to improve future task performance.

Perhaps more importantly, we found that there was an interactive effect of accuracy and ambiguity. In other words, there was an interaction such that these regions showed greater activity for ambiguous than clear trials, and this effect was more robust on error than correct trials. Previous work presented a model of cingulo-opercular task control, modified from Dosenbach et al. (2007), suggesting that several types of performance reporting signals, including errors, ambiguity/conflict, and reaction time, can be computed in the cingulo-opercular regions at once (Neta et al. 2014). We provide further evidence here that the cingulo-opercular system can accept or compute, and presumably utilize, many forms of performance reporting in the service of providing more effective top-down signals in later trials, or later epochs, or for the performance of similar tasks in the future.

Finally, we provide evidence that these cingulo-opercular signals are important for performance reporting. Specifically, there was a relationship between these signals and task performance. First, we found that, following trials with greater a cingulo-opercular response (error, ambiguity), task performance was improved. Importantly, these effects were specific to errors and ambiguity, as there was no significant relationship between performance and activity on clear correct trials. Second, there were individual differences relating brain activity to task performance, such that individuals that recruit greater activity in these regions also show better behavioral performance.

Cingulo-opercular Regions in the Literature: Conflict, Predictions, and Actions

These data not only inform the error- and ambiguity-related processes in the cingulo-opercular network, but can also work toward informing and, in some cases, contradicting extant theories of ACC function. We focus here on ACC because these theories are more thoroughly spelled out in the literature, and we believe these findings spread to bilateral aI/fO, which is functionally coupled with ACC across tasks and rest. Some of the more prominent theories suggest that ACC is important for conflict monitoring (Botvinick et al. 2001), others suggest a role in prediction of response outcomes (Alexander and Brown 2011), and other suggests ACC is responsible for action monitoring (Rushworth et al. 2004). It is important to mention here, first, that the region under discussion extends dorsally from the ACC to the medial superior frontal cortex. Recent work has

demonstrated that much of the literature discussing ACC points to a region, like ours, dorsal to cingulate cortex (Lieberman and Eisenberger 2015). In this work, the authors showed that a search of the literature using Neurosynth found that both search terms "dACC" and "anterior cingulate" resulted in activation maps that included this more dorsal region (but see commentary on methodological issues with the approach; https://tinyurl.com/nvt3vlr, as well as a response suggesting this may be partly related to variation in cingulate anatomy; 10.6084/m9.figshare.2026014). To be more specific, the original model presented by Brown and Braver (2005) focused on a similar region dorsal to the ACC. Since then, other papers have contributed to the ACC debate while discussing the same region that extends dorsally to the medial superior frontal cortex (e.g., O'Reilly et al. 2013).

Having said that, we address the varied theories about ACC function in turn here, demonstrating that our present data are, at least in part, incompatible with the existing theories. First, the conflict monitoring model might predict that ambiguity begins low and then ramps up with additional information as multiple response candidates compete (before a response is made), diminishing only when a single response has been chosen. This is not consistent with the present findings, since we have shown that activity in these regions stays low until the end of the trial, at which point a single response has been chosen. Indeed, an extension of the conflict monitoring model has proposed that conflict occurs on correct trials when an erroneous response is prepared but the correct response manages to override it (i.e., conflict occurs prior to the response, or early in the trial; Coles et al. 1988; Kopp et al. 1996). On error trials, in contrast, the model suggests that conflict occurs after the response is made. Taken together, this model would suggest a temporal dissociation between error- and conflict-related signals in ACC, which is not supported by the present work. In this way, this report contradicts at least one form of the conflict monitoring model.

Second, the prediction of response outcomes (PRO) model suggests that the ACC calculates the discrepancy between predictions and outcomes, where the signals are scaled by the degree to which outcomes violate predictions. As a result, this model provides a unifying account of prediction, error, and learning effects that have been localized to the ACC (Alexander and Brown 2011). Some support for this theory comes from paradigms that take a similar approach to the present work, attempting to dissociate conflict and errors (Nee et al. 2011) and predictions and outcomes (Jahn et al. 2014). However, we found an increased response for errors on ambiguous as compared to clear trials. The PRO model would predict, instead, that errors on ambiguous trials would have less prediction error than errors on clear trials. In these ways, we also contradict the PRO model. Further, this model explicitly argues that activity should ramp up over time: "cell activities representing the outcome probabilities grow larger as the timing of the expected outcome approaches. If the expected outcome is unexpectedly delayed, "then the activity predicting the outcome will continue to increase until the outcome actually occurs," at which point the prediction activity will cease." (Brown 2011). In other words, the PRO model predicts that activity increases starting early in the trial, and continues to increase "until" a response is made. The present findings suggest something quite different; activity does not begin to increase until "after" a response is made. This is not consistent with the response profile reported here, where activity stay lows until the end of the trial.

Despite an overwhelming preoccupation with the error- and conflict-related signals in ACC, other research has emphasized a broad role in encoding the relationship between an action and the reinforcement value of its outcome, regardless of when the outcome is a positive reward or an error (Rushworth et al. 2004; Shenhav et al. 2013). In other words, the ACC does not just encode which outcome is expected (e.g., whether an action is expected to lead to an error), it is proposed to also be a crucial part of a system for encoding whether or not an action is worth performing given both the value of the expected outcome and the cost of performing the action. Shenhav et al. (2013) specifically includes roles of both prospection (estimating value of control) and evaluation. This suggests, as with the previous models, that the activity in this region must, at least in part, come online early (before an action is made) in an effort to determine whether an action should be taken. As such, our data do not support this model in its entirety. Further, because this model predicts that this region is important for relating actions to outcomes that are both positive (reward) and negative (error-related), this model might predict that activity would be greater on ambiguous than clear trials, regardless of whether the response made was correct or an error. This is also inconsistent with the present data, and thus we can rule out these models as well.

Relatedly, other models (Behrens et al. 2007; O'Reilly et al. 2013) demonstrated a role for the ACC in updating action values or internal models from which future action is generated, which is not incompatible with our findings, provided that the updating process occurs late in the trial. However, they go on to assert that the ACC may be loosely related to other models suggesting a role in exploration and foraging (Kolling et al. 2012) or learning rates (Behrens et al. 2007), which implies a role in early stages of a trial when new information or evidence is accumulated. This explanation, then, is not compatible with our findings, as we would predict that the cingulo-opercular regions are important for reporting, but not online monitoring or learning preceding, outcomes. We believe that this other work relates more to an adaptive type of control rather than reporting outcomes, as we propose is performed by the cingulo-opercular regions.

An alternative to these models would be that the cingulo-opercular regions are attuned to multiple types of performance signals, including errors and ambiguity/conflict, and that these regions are reporting on these signals at the end of the trial, in order to improve future task performance. In this way, they offer something in the way of performance reporting across many types of performance signals and many types of tasks domains.

Cost and Benefit of the Current Design

Interestingly, this experimental design allowed us to generalize previous work demonstrating that the cingulo-opercular regions show greater activity for ambiguous than clear trials in a variety of domains, including ambiguity of emotional valence, semantics, and phonology. However, there is one limitation in this generalization: ambiguity in the present experiment is resolved once the black mask is completely degraded and the object is fully revealed to the participant. However, in previous work using emotional valence (Neta et al. 2013) and semantics and phonology (Neta et al. 2014), the ambiguity of the stimulus is derived from a dual representation. For example, unlike happy and angry facial expressions, which are consistently associated with clear positivity and negativity, respectively, surprised facial expressions are associated with both positive (e.g., a surprise birthday party) and negative (e.g., witnessing a car accident) outcomes. As such, when these expressions are presented in the absence of clarifying contextual information, they are interpreted as positive by some people and as negative by others, where both

possible responses are considered to be correct (see Kim et al. 2003; Neta et al. 2009; Neta and Whalen 2010; Neta et al. 2013). Similarly, when asked to classify the word "SAFE" as either abstract or concrete, one might think of a safe for storing valuables, and another might think of the absence of danger. In both of these types of ambiguity, there are multiple representations for a single stimulus, and the ambiguity is only subjectively resolved once a participant makes a decision about the stimulus (i.e., there is no "correct" answer). In other words, the ambiguity is not resolved through the presentation of additional information over the course of the trial, as is the case in the present slow reveal design. In order to deal with this, we encouraged participants to respond to each stimulus as early as possible, once they have a relatively confident guess as to the identity of the object that was being revealed. Further, if participants did not make a response until the image is fully revealed (i.e., when the ambiguity is resolved), then the trial is coded as an omission and removed from subsequent analyses. Given all of this, we believe that this extended trial design is the best current way to examine the responses to ambiguity- and accuracy-related effects over the course of a trial, and to differentiate effects that takes place early in the trial, as evidence is being accumulated, from those that come online at or near the end of the trial, at the moment of decision. Further, as is briefly mentioned in the Introduction, this subtly different definition of ambiguity affords us the benefit of examining the interaction effects of accuracy and ambiguity. In other words, we previously showed that the cingulo-opercular regions appear to monitor both accuracy and ambiguity effects (Neta et al. 2014). But the present data take this one step further to show that there are interactive effects of accuracy and ambiguity: there was greater activity for ambiguous than clear trials, and this effect was more robust on error than correct trials.

Second, the error-related responses have some temporal ambiguity in that, for T_Rs 5/6, there is a limited set of times that the error can be realized. For example, assuming that error-related activity may be, at least in part, associated in time with when the participant becomes "aware" of the error, an erroneous decision made at T_R 6 could only be realized immediately or at T_R 7 (during the full reveal). Given the temporal blurring of the hemodynamic response, these times are roughly equivalent, producing a reasonably systematic response regardless of when the error-related activity truly begins. In contrast, a decision made at T_R 3 could produce error-related activity at any of T_Rs 4–7. This length is well beyond the range of the hemodynamic blurring, so activity occurring at different times within this window will not neatly sum in amplitude. Hence, if the error-related activity is more temporally ambiguous for ambiguous than clear trials for decisions occurring at TRs 3/4 (where error-awareness may take longer for ambiguous trials, since the participant may need more information from the image to realize the error), then one would expect a more broadened response profile for ambiguous trials, which coincidentally, also reduces the peak activity (as is shown in Supplementary Fig. 2). In other words, the error-related activity occurs at different points in different trials and averaging across the trials may dampen the peak response. Future studies could probe these effects using a slightly modified task where participants are asked to make a second response if/when they realize they have made an error. Having said that, this conflates error-related activity with error-awareness, which are not always one and the same. Indeed, many error-related signals can happen in the absence of clear awareness on the part of the subject (Nieuwenhuis et al. 2001).

Finally, it is important to mention that these findings are not contradictory with other reports showing ACC responses to reward (cost, benefits) and other performance-related signals. Indeed, we would predict that the cingulo-opercular regions would report on a variety of such outcomes, but that they would report on these outcomes at the end of the trial, and not take part in running the cost and benefit analysis during the early stages of the trial. In this way, we would predict that cingulo-opercular responses that come online during trials where cost/benefit analysis is done, the signal would be similar to that of ambiguity, where the cingulo-opercular regions do not come online to help resolve the ambiguity (while the participant is selecting between competing alternatives), but rather these regions report on the outcome of the trial after the response has been made. Given that much, if not all, of this previous work did not use an experimental design that allows for analyzing these temporal characteristics, we see these effects as complementary.

Conclusions

The present work builds on previous findings using an extended trial to examine the stages of recognition processes in situations of ambiguity using fMRI. Other recent work has used intracranial recordings to examine these processing stages for ambiguous as compared with clear objects (Cho-Hisamoto et al. 2015). Here, we have found that the same regions that appear to show multiple types of task-control signals in the cingulo-opercular network (see Dosenbach et al. 2006; Neta et al. 2014), withhold information until the moment of recognition. Further, there is a relationship between these signals and task performance, such that (1) trials that elicit greater cingulo-opercular activity (e.g., errors) are followed by improved behavioral performance on the subsequent trial, and (2) individuals that show greater activity in these regions also show better behavioral performance. This combination of results fits much more cleanly with a performance reporting explanation than other components of task control (e.g., online monitoring). We do not mean to imply here that there is (or that there should be) a single process explanation for the regions in the cingulo-opercular network (including the dACC and the aI/fO), or for any other brain region (see also, Neta et al. 2014). Instead, we suggest that these signals are important for computing and utilizing multiple types of performance reporting signals (including but "not limited to" error, ambiguity, reaction time), in the service of improving future task performance. Finally, these signals may include a number of other variables not manipulated in the present work.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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