Neuronal correlates of metacognition in primate frontal cortex

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SUPPLEMENTAL INFORMATION

Supplemental Figures

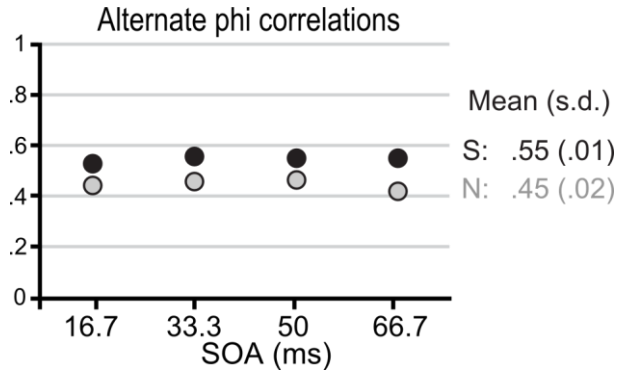

Figure S1. Results of alternate calculation for phi correlations (Related to Figure 1). This alternate method (Zar, 1999), takes into account whether the correlations are positive or negative. Conventions as in Figure 1c.

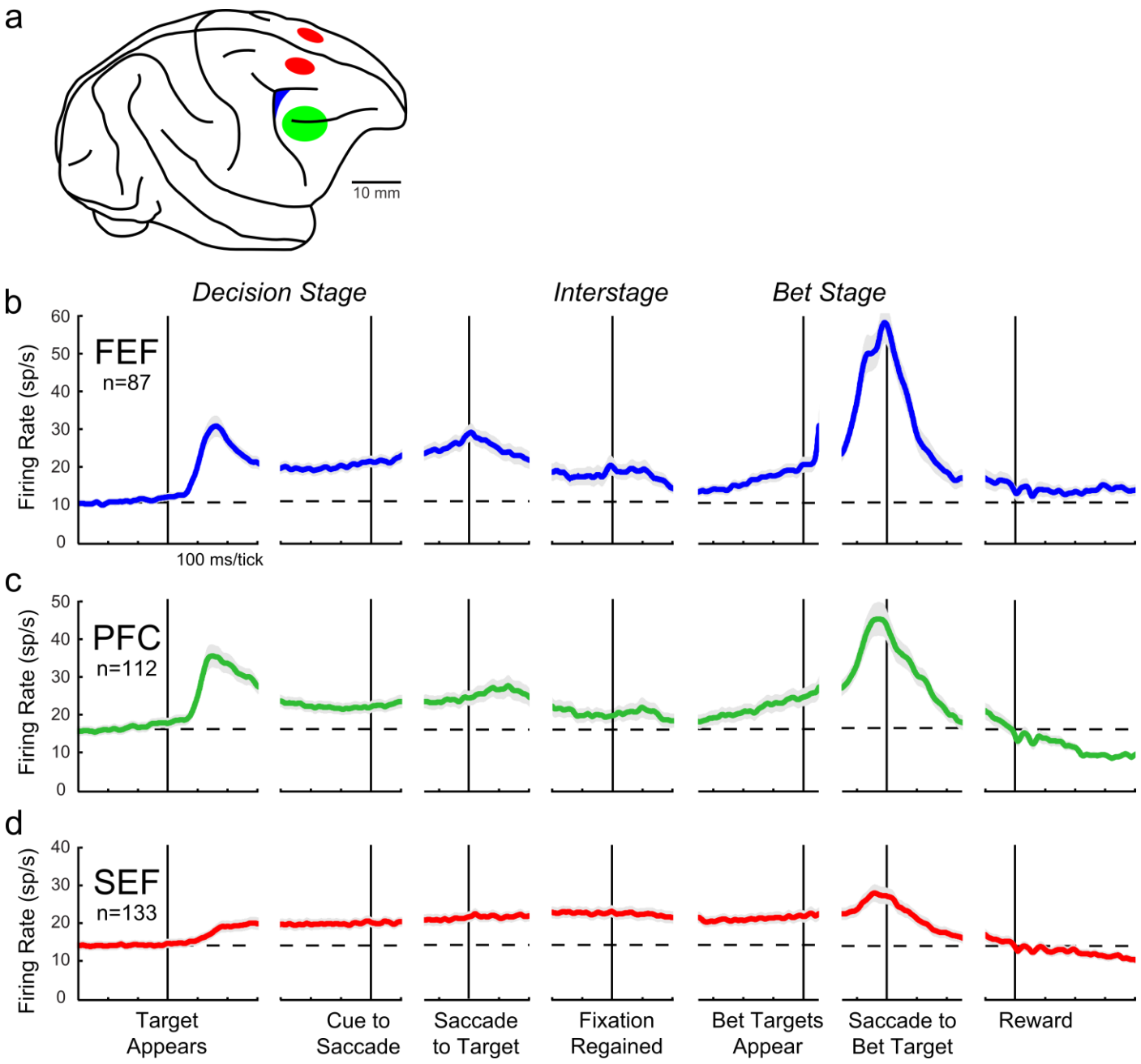

Figure S2. Populations of neurons recorded from FEF, PFC, and SEF (Related to Figure 2). (a) Summary of recording locations: right FEF (blue; in anterior bank of arcuate sulcus), right PFC (green; posterior third of entire PFC), and both SEFs (red). All of the sites were tested in both monkeys. (b-d) Overall activity profiles for our FEF, PFC, and SEF neuronal populations during the metacognition task. All trial outcomes and directions pooled. Traces show mean firing rates (lines) and SEM boundaries (shading) aligned to each task event.

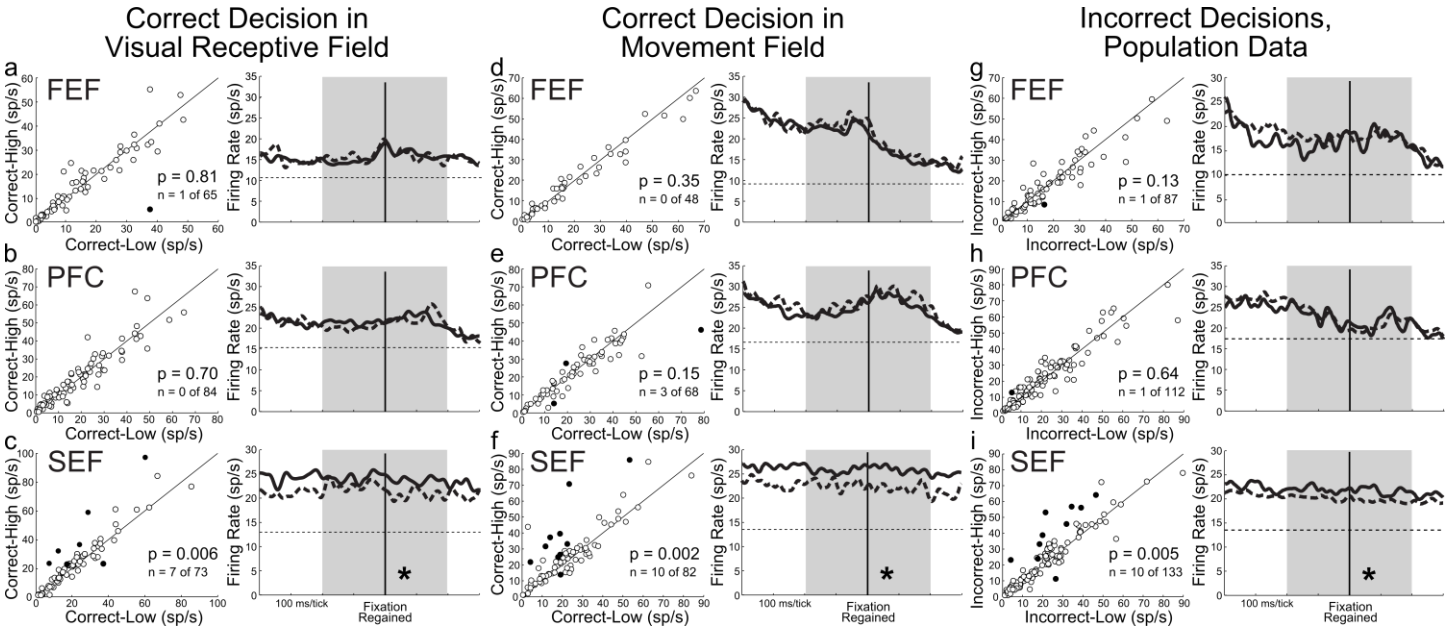

Figure S3. Further analyses of metacognition-related activity in SEF (Related to Figure 3). (a-c) Scatterplots (left) show CH vs. CL firing rates for each neuron in the FEF, PFC, and SEF, restricted to those neurons with an identifiable visual receptive field, and to trials involving the single targets placed most optimally in that receptive field. Other details as in Figure 3d-f. (d-f) Same as (a-c), but restricted to neurons with an identifiable movement field and trials involving the single targets placed most optimally in that movement field (hence correct saccades were made into the movement field). (g-i) Comparison of IH vs. IL activity during the interstage epoch (same conventions as Figure 3d-f; this is the analog of the CH vs. CL analyses in the main text).

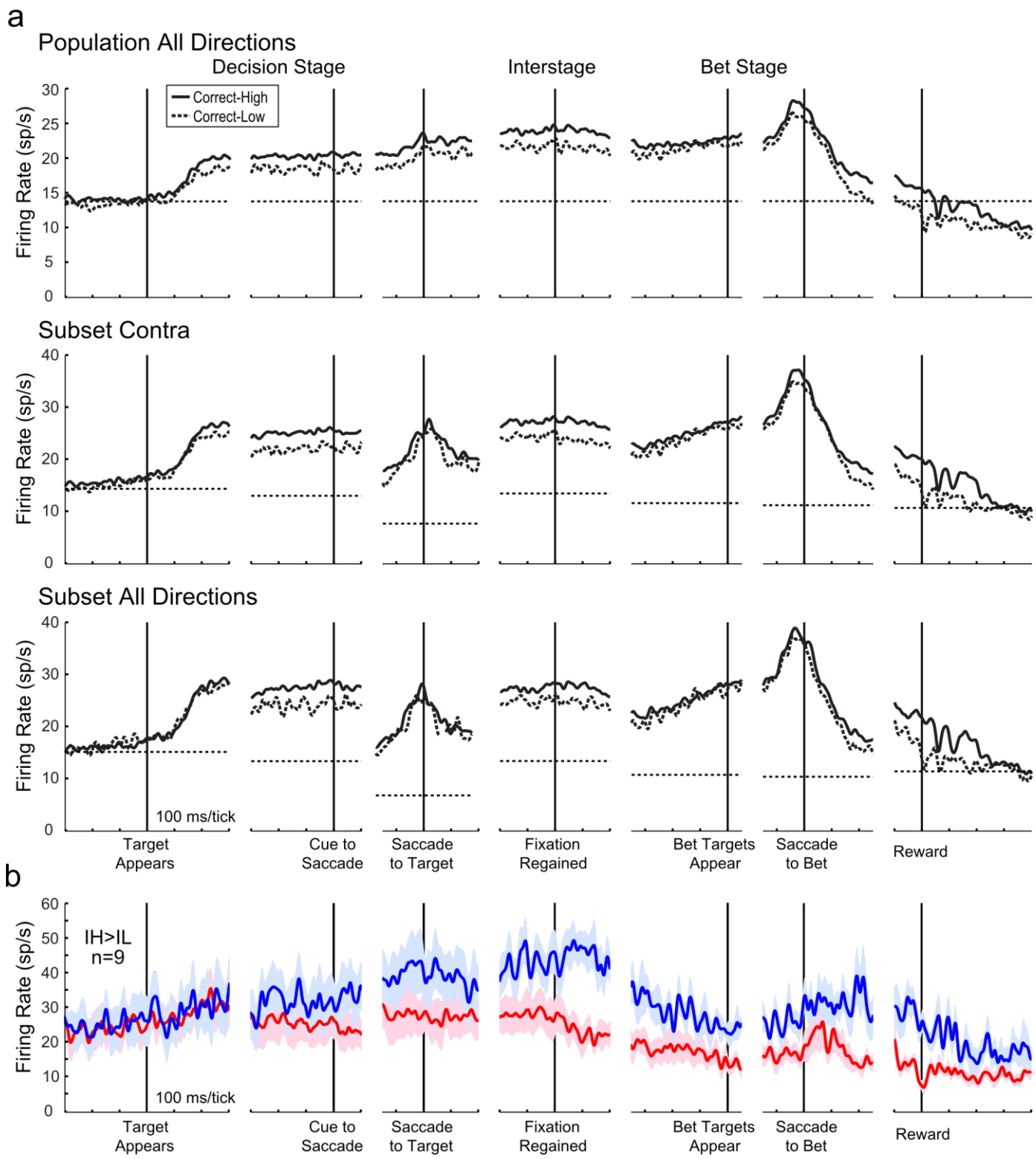

Figure S4. Further analyses of SEF population activity (Related to Figure 5). (a) *Top*: Population data pooled over all directions. *Middle*: Subset of neurons significantly active in each epoch, analyzed by contralateral hemifield. *Bottom*: Same, but analyzed for all directions. (b) The 9 SEF neurons for which IH activity was greater than IL activity during the interstage epoch.

Supplemental Tables

Saccade Latencies

Outcome	Correct-High	Correct-Low	Incorrect-High	Incorrect-Low
Monkey N	222.3	221.7	237.8	231.9
Monkey S	167.4	163.6	174.2	177.5

Table S1. Latencies to saccade onset (in ms) during the Decision Stage for each monkey, across each trial outcome. Latencies did not differ for either animal between Correct-High vs. Correct-Low trials or between Incorrect-High vs. Incorrect-Low trials, $p > .05$ for all, Holm-Sidak multiple comparison tests.

Proportions of Trial Outcomes

SOA	Correct-High	Correct-Low	Incorrect-High	Incorrect-Low
Monkey N				
16.7	0.68 (0.20)	0.32 (0.09)	0.19 (0.14)	0.81 (0.57)
33.3	0.68 (0.27)	0.32 (0.12)	0.21 (0.13)	0.79 (0.48)
50.0	0.68 (0.37)	0.32 (0.18)	0.19 (0.09)	0.81 (0.36)
66.7	0.67 (0.44)	0.33 (0.22)	0.20 (0.07)	0.80 (0.27)
Monkey S				
16.7	0.67 (0.21)	0.33 (0.11)	0.26 (0.18)	0.74 (0.50)
33.3	0.67 (0.26)	0.33 (0.13)	0.25 (0.15)	0.75 (0.46)
50.0	0.70 (0.39)	0.30 (0.16)	0.23 (0.10)	0.77 (0.34)
66.7	0.75 (0.53)	0.25 (0.17)	0.22 (0.07)	0.78 (0.23)
Both Monkeys				
All SOAs	0.71 (0.35)	0.29 (0.14)	0.20 (0.10)	0.80 (0.41)

Table S2. Proportions of trial outcomes for each monkey and SOA and, in bottom row, for the overall pooled data. The first number in each table entry is the proportion of Correct-High or Correct-Low trials vs. all Correct trials, or Incorrect-High or Incorrect-Low trials vs. all Incorrect trials. The parenthetical number in each entry shows the proportion of CH, CL, IH, or IL trials relative to all trials. In the bottom row, each number is not necessarily the average of the numbers above it, due to rounding errors and unequal data from each monkey.

Decision-related Activity: Population Subsets

FEF	Baseline	Visual-1	Delay	Presaccadic-1	Postsaccade
n		63	52	41	19
Correct	10.4 (0.9)	33.0 (2.2)	25.9 (2.1)	44.4 (3.5)	39.4 (6.4)
Incorrect	10.2 (0.9)	28.5 (1.9)	21.7 (2.0)	44.7 (4.0)	37.4 (6.4)
p	.33	**< .001***	**< .001***	.81	.44
PFC					
n		80	54	25	20
Correct	16.0 (1.3)	42.4 (3.2)	32.8 (2.6)	47.7 (6.0)	40.8 (8.0)
Incorrect	16.4 (1.3)	37.4 (3.1)	26.0 (2.4)	43.0 (5.2)	39.9 (8.4)
p	.47	**< .001***	**< .001***	.10	.64
SEF					
n		68	76	27	46
Correct	13.4 (1.1)	23.5 (2.3)	26.5 (2.0)	26.1 (3.0)	28.8 (2.4)
Incorrect	13.1 (1.1)	21.0 (2.1)	21.2 (1.6)	25.3 (2.9)	24.1 (2.2)
p	.20	**< .001***	**< .001***	.28	**< .001***

Table S3. Same as Table 1, but for the subsets of neurons within each epoch that had increased activity relative to baseline. For each cortical region, the number (n) of included neurons in each epoch is listed, and all correct vs. all incorrect firing rates (spikes/s) are shown with standard errors in parentheses and paired t-test p-values underneath. Asterisks and bold fonts represent significant differences ($p < .05$) between correct and incorrect trials.

Bet-related Activity: Population

FEF	Baseline	Visual-1	Delay	Presaccadic-1	Postsaccade
High	10.3 (0.9)	25.9 (1.9)	18.7 (1.5)	29.3 (2.6)	19.6 (2.3)
Low	10.3 (0.9)	24.4 (1.7)	18.1 (1.5)	30.5 (2.8)	20.7 (2.4)
p	.83	**.006***	.31	.42	.16
PFC					
High	16.0 (1.3)	32.7 (2.5)	22.6 (1.6)	25.6 (2.2)	25.8 (2.4)
Low	16.5 (1.3)	31.4 (2.4)	21.4 (1.5)	25.4 (1.9)	26.0 (2.3)
p	.20	**.003***	**.020***	.82	.62
SEF					
High	13.3 (1.1)	18.2 (1.4)	19.9 (1.5)	22.3 (1.5)	22.5 (1.5)
Low	13.2 (1.1)	17.5 (1.3)	17.5 (1.3)	20.8 (1.4)	20.6 (1.3)
p	.40	**.036***	**< .001***	**.013***	**.001***

Table S4. Population bet-related firing rates during Decision Stage epochs. For each cortical region, all high bet vs. all low bet firing rates (spikes/s) are shown with standard errors in parentheses and paired t-test p-values underneath. Asterisks and bold fonts represent significant differences ($p < .05$) between high and low bet trials.

Bet-related Activity: Population Subsets

FEF	Baseline	Visual-1	Delay	Presaccadic-1	Postsaccade
n		63	52	41	19
High	10.3 (0.9)	31.7 (2.1)	24.8 (2.0)	44.4 (3.6)	38.4 (6.3)
Low	10.3 (0.9)	29.3 (2.0)	22.4 (2.1)	43.8 (3.8)	38.3 (6.4)
p	.83	**.001***	**.001***	.69	.97
PFC					
n		80	54	25	20
High	16.0 (1.3)	40.6 (3.2)	30.8 (2.6)	49.0 (6.3)	40.9 (8.0)
Low	16.5 (1.3)	38.4 (3.1)	27.3 (2.4)	42.2 (4.6)	39.4 (8.1)
p	.20	**< .001***	**< .001***	**.019***	.32
SEF					
n		68	76	27	46
High	13.3 (1.1)	22.8 (2.2)	25.8 (2.0)	26.2 (3.0)	27.7 (2.4)
Low	13.2 (1.1)	21.9 (2.1)	22.2 (1.8)	25.2 (3.0)	24.5 (2.1)
p	.40	.11	**< .001***	.26	**.001***

Table S5. Same as Table S4, but for the subsets of neurons within each epoch that had increased activity relative to baseline. For each cortical region, the number (n) of included neurons in each epoch is listed, and all high bet vs. all low bet firing rates (spikes/s) are shown with standard errors in parentheses and paired t-test p-values underneath. Asterisks and bold fonts represent significant differences ($p < .05$) between high and low bet trials.

Metacognition-related Activity: Comparisons between Monkeys

Monkey	Neuronal Sample	Individual Neurons Significant	CH Firing Rate	CL Firing Rate	CH-CL p value
S	All	31% (22/72)	26.6 (2.2)	23.1 (1.7)	**.003***
	Active	40% (19/47)	29.2 (2.4)	24.5 (1.8)	**.001***
N	All	10% (6/61)	20.5 (2.3)	19.5 (2.3)	**.002***
	Active	14% (6/42)	23.8 (2.7)	22.6 (2.7)	**.001***

Table S6. Each monkey's metacognition-related SEF activity data during the interstage epoch, analyzed over all directions. Within each row corresponding to data from one monkey, the results of analyzing all neurons are presented above the results of analyzing only the neurons significantly active during the interstage epoch. Average firing rates (spikes/s) are shown with standard errors in parentheses. Asterisks and bold fonts represent significant differences of paired t-tests ($p < .025$).

Bet Stage-related Activity: Population

FEF	Visual-2	Presaccadic-2	Reward Anticipation	Reward
CH	49.9 (4.6)	50.8 (4.7)	16.9 (2.0)	11.5 (1.4)
CL	51.3 (4.5)	53.6 (4.8)	18.9 (2.0)	12.8 (1.3)
p	.35	.13	**.005***	.16
PFC				
CH	43.5 (3.8)	44.3 (4.0)	23.8 (2.1)	11.7 (1.2)
CL	44.1 (4.0)	44.3 (4.0)	26.1 (2.3)	12.4 (1.1)
p	.71	.99	.04	.28
SEF				
CH	27.2 (2.2)	27.8 (2.2)	19.1 (1.6)	12.0 (1.4)
CL	26.1 (2.1)	27.6 (2.4)	16.4 (1.6)	10.3 (1.2)
p	.10	.80	**< .001***	**.002***

Table S7. Population Bet Stage-related firing rates. For each cortical region, all Correct-High (CH) vs. all Correct-Low (CL) firing rates (spikes/s) are shown with standard errors in parentheses and paired t-test p-values underneath. Asterisks and bold fonts represent significant differences ($p < .025$) between CH and CL trials.

Bet Stage-related Activity: Population Subsets

FEF	Visual-2	Presaccadic-2	Reward Anticipation	Reward
n	64	63	33	25
CH	59.2 (5.0)	61.1 (5.1)	29.8 (3.5)	20.6 (3.0)
CL	61.2 (4.7)	64.2 (5.2)	31.9 (3.4)	18.9 (2.5)
p	.29	.17	.08	.39
PFC				
n	77	72	65	17
CH	57.2 (4.6)	62.0 (5.0)	32.5 (2.9)	26.7 (4.3)
CL	58.2 (4.8)	62.2 (4.9)	34.3 (3.2)	22.5 (3.5)
p	.66	.93	.30	**.016***
SEF				
n	72	69	63	28
CH	35.1 (2.9)	37.8 (3.0)	25.5 (2.5)	22.6 (4.2)
CL	33.9 (3.0)	37.5 (3.5)	21.6 (2.6)	18.9 (3.9)
p	.23	.85	**.002***	**.018***

Table S8. Same as Table S7, but for the subsets of neurons within each epoch that had increased activity relative to baseline. For each cortical region, the number (n) of included neurons in each epoch is listed, and all Correct-High (CH) vs. all Correct-Low (CL) firing rates (spikes/s) are shown with standard errors in parentheses and paired t-test p-values underneath. Asterisks and bold fonts represent significant differences ($p < .025$) between CH and CL trials.

SEF Activity Preceding High Bets (CH vs. IH) or Low Bets (CL vs. IL) in Decision Stage and Interstage

	Population	Baseline	Visual-1	Delay	Presaccadic-1	Postsaccade	Interstage
High Bets	CH	13.6 (1.1)	18.5 (1.4)	20.1 (1.6)	22.2 (1.5)	22.9 (1.5)	23.6 (1.6)
	IH	13.6 (1.1)	16.9 (1.4)	17.3 (1.3)	20.8 (1.6)	21.5 (1.5)	21.4 (1.6)
	p	.49	**.002***	**< .001***	.04	**.004***	**.01***
	Subset						
	n		62	72	30	42	90
	CH	13.6 (1.1)	24.5 (2.4)	27.9 (2.2)	24.0 (2.7)	27.8 (2.7)	27.8 (2.0)
	IH	13.6 (1.1)	21.9 (2.4)	21.4 (1.9)	25.4 (3.2)	24.9 (2.4)	23.1 (1.0)
	p	.49	**.003***	**< .001***	.30	**.008***	**< .001***
	Population						
Low Bets	CL	13.1 (1.2)	17.7 (1.5)	18.6 (1.4)	20.1 (1.4)	21.0 (1.4)	21.3 (1.5)
	IL	13.0 (1.1)	16.8 (1.3)	17.0 (1.2)	20.5 (1.4)	20.4 (1.4)	19.6 (1.4)
	p	.86	.23	**.046***	.69	.08	**.01***
	Subset						
	n		62	72	30	42	90
	CL	13.1 (1.1)	24.3 (2.5)	24.2 (2.1)	22.7 (2.8)	27.8 (2.7)	25.2 (1.8)
	IL	13.0 (1.1)	21.6 (2.2)	21.4 (1.7)	20.8 (2.3)	23.1 (2.3)	21.2 (1.7)
	p	.86	**.004***	**.024***	.63	**.003***	**< .001***

Table S9. SEF firing rates compared between correct and incorrect high bet trials (CH vs. IH), *top section*, and correct and incorrect low bet trials (CL vs. IL), *bottom section*, during the Decision Stage and the Interstage epoch. Within each High or Low Bets section, results from the total population (upper row) and the subset of neurons with significant activity in each epoch (lower row) are shown separately. For each epoch (columns), firing rates for correct and incorrect trials are shown (spikes/s) with standard errors in parentheses and compared using paired t-tests (p-values underneath). Asterisks and bold fonts represent significant differences ($p < .025$) between data for which the same eventual reward was anticipated, but after different decisions.

SEF Activity During High Bets (CH vs. IH) or Low Bets (CL vs. IL) in Bet Stage and Reward Period

	Population	Visual-2	Presaccadic-2	Reward Anticipation	Reward
High Bets	CH	27.2 (2.2)	27.9 (2.2)	19.1 (1.6)	12.0 (1.4)
	IH	25.3 (2.0)	26.2 (2.2)	18.6 (1.6)	16.1 (1.6)
	p	**.007***	.05	.62	**<.001***
	Subset				
	n	72	69	63	28
	CH	35.1 (2.9)	37.8 (3.0)	25.5 (2.5)	22.6 (4.2)
	IH	31.6 (2.7)	34.1 (3.2)	21.9 (2.2)	24.7 (4.5)
	p	**< .001***	**< .004***	**.018***	.63
	Population				
Low Bets	CL	26.1 (2.1)	27.6 (2.4)	16.4 (1.6)	10.3 (1.2)
	IL	24.8 (2.1)	26.1 (2.4)	16.8 (1.6)	11.0 (1.3)
	p	.10	.11	.43	.04
	Subset				
	n	72	69	63	28
	CL	33.9 (3.0)	37.5 (3.5)	21.6 (2.6)	18.9 (3.9)
	IL	31.0 (3.0)	35.3 (3.5)	20.9 (2.6)	18.5 (3.9)
	p	**.019***	.16	.27	.61

Table S10. Same as Table S9, but for Bet Stage and Reward periods.

Supplemental Results

Bet-related activity

We analyzed bet-related activity by comparing all high bet versus all low bet activity during the Decision Stage. Considering that behavioral analyses showed that most correct (or incorrect) decisions were followed by high (or low) bets, we expected that bet-related activity would parallel decision-related activity. This prediction was confirmed. For each cortical region, population activity in both the visual-1 and delay epochs predicted the eventual bets (except for the FEF delay period; Table S4). During saccade-related periods, SEF activity predicted bets but neither FEF nor PFC did. For the subsets of neurons specifically active in the epochs (Table S5), activity in all three areas predicted bets in both the visual-1 and delay epochs (except the SEF visual-1 period) and for saccade-related epochs, SEF postsaccadic and PFC presaccadic-1 activity predicted bets.

Spike Burstiness

The CH > CL and CH < CL subsets could consist of differing neuron phenotypes, as suggested by their differing overall activity levels. Inhibitory interneurons ("fast spiking" neurons) tend to have higher spontaneous and task-related firing rates than pyramidal ("regular spiking") neurons (e.g. Connors and Gutnick, 1990; Mitchell et al., 2007). We could not perform the standard test for distinguishing between fast spiking and regular spiking neurons (comparisons of action potential widths; e.g. Mitchell et al., 2007), so we conducted a test on spiking statistics instead: burstiness analysis. Anderson et al. (2011) demonstrated that in primate cerebral cortex, putative inhibitory neurons (as identified with action potential width analysis) show a lower incidence of burstiness and lower median burstiness than putative pyramidal neurons. For the 20 neurons in our CH > CL and CH < CL subsets, we calculated each neuron's burstiness/refractory index (BRI), which summarizes how often a neuron fires spikes in quick succession (Anderson et al., 2011). Briefly, a shift predictor (mean cross-correlation of all trials for the neuron) was subtracted from the neuron's auto-correlation, and then that number was divided by the standard deviation of the shift predictor. The result, the BRI, is

analogous to a z-score; its units are in standard deviations, and a neuron with BRI > 2 was considered significantly bursty. We calculated BRI for spike trains during two epochs: the baseline epoch, when activity was as "spontaneous" (non-task-related) as possible, and the interstage epoch, when the main task-related function of interest, metacognition, occurred (analogous to the attentional, "sustained" period tested by Anderson et al., 2011). Data were collapsed over all trial outcomes.

We found no evidence from burstiness analysis to support the hypothesis that the CH > CL and CH < CL subsets consisted of different neuronal phenotypes. The *incidence of bursty neurons* in the baseline epoch was 64% (9/14 neurons) for the CH > CL subset and 83% (5/6 neurons) for the CH < CL subset. In the interstage epoch, the incidence was 78% (11/14 neurons) and 50% (3/6 neurons) respectively. In neither epoch was the incidence of bursty neurons significantly different between the two subsets (Fisher Exact Tests, $p > .3$ for both). The *median BRI* in the baseline epoch was 4.22 for the CH > CL subset and 9.40 for the CH < CL subset. In the interstage epoch, the medians were 8.72 and 4.80 respectively. In neither epoch was BRI significantly different between the two subsets (Mann-Whitney *U* tests, $p > .5$ for both). These negative results should be considered with caution, because small numbers of neurons were analyzed and burstiness alone (without action potential width data) is a weak predictor of neuronal phenotype (Anderson et al., 2011). Larger samples of metacognition-related SEF neurons that include action potential waveform data are needed to fully test the hypothesis that the CH > CL and CH < CL subsets consist of different neuronal phenotypes.

IH versus IL

The complementary approach to testing whether neuronal activity correlates with metacognitive behavior is to compare Incorrect-High (IH) and Incorrect-Low (IL) trials. As noted in the main text, because the target location was by definition not coincident with the saccade destination in incorrect trials, and because IH trials were rare, analysis of IH and IL trials was not as straightforward as for CH and CL trials. We separated the IH vs. IL analysis into a sensory-related activity comparison (visual-1 and delay epochs) and a motor-related

activity comparison (presaccadic-1 and postsaccadic epochs) as in our analysis of decision related activity. We used the motor-related activity comparison method to analyze the interstage epoch, because this epoch was during a time when the monkey's gaze returned to the center of the screen after making its (erroneous) decision saccade.

For the critical interstage epoch, our analysis of IH vs. IL trials yielded similar results as our analysis of CH vs. CL trials. The SEF population exhibited differential activity during the interstage epoch for IH vs. IL trials (IH: 21.4 ± 1.6 sp/s, IL: 19.6 ± 1.4 sp/s, $p = .005$), but the PFC and FEF populations did not. None of the cortical regions showed differential activity between IH and IL trials during the visual-1, delay, and presaccadic-1 periods. In the postsaccadic epoch neither the SEF nor PFC showed an effect, and the FEF showed a reverse effect; as a population, it was less active for IH trials than IL trials (IH: 19.0 ± 2.6 sp/s, IL: 21.97 ± 2.9 sp/s, $p = .008$). Finally, we repeated these analyses using only the subsets of neurons with significant activity in the given epochs. The SEF was again differentially active during the interstage epoch (IH: 23.1 ± 1.0 sp/s, IL: 21.18 ± 1.7 sp/s, $p = .02$), but the PFC and FEF were not. None of the remaining comparisons were significant.

Bet Stage-related activity

We analyzed the neuronal activity after the interstage epoch, through the Bet Stage, to the end of the trial. It is clear from inspection that, as the monkeys awaited the appearance of the bet targets, differential CH-CL activity in the SEF population waned (Figure 5c, range before "Bet Targets Appear"). Quantitatively, we found that none of the three cortical regions differentiated CH-CL or IH-IL in their visual responses to the bet targets (visual-2 epoch) or in their activities associated with saccades to the bet targets (presaccadic-2 epoch; paired t-tests, all $p > .025$). This held true for total population analyses (CH vs. CL data are shown in Table S7), and for the subsets of neurons that had increased activity relative to baseline (CH vs. CL data are shown in Table S8).

The SEF population activity became differentially modulated again after the monkeys placed their bets, in the reward anticipation and reward epochs (Tables S7 and S8; also apparent in Figure 5c, "Saccade to Bet" and "Reward" alignments). Comparable effects in the FEF and PFC were rare (significant only for the FEF population during the reward anticipation period, Table S7, and the PFC subset during the reward period, Table S8). For IH-IL comparisons, the SEF and PFC total populations had greater firing rates for IH trials during the reward epoch (SEF: IH: 16.1 ± 1.6 sp/s, IL: 11.0 ± 1.3 sp/s, $p < .001$; PFC: IH: 15.91 ± 1.5 sp/s, IL: 11.0 ± 1.0 sp/s, $p < .001$), but no other effects were significant (not shown).

Supplemental Discussion

Riskiness

Differences in neuronal activity between trial outcomes could have been related to riskiness of high vs. low bets. Were this the case, one would predict CH and IH trials to both have greater firing rates than CL and IL trials. Our analyses in the main text demonstrated that CH trials had greater firing rates than CL trials, and that IH trials had greater firing rates than IL trials, both of which are consistent with riskiness as an explanation. IH and CL trials, however, were not significantly different in any epoch throughout the trial (paired t-tests, all $p > .025$) except in the reward epoch (after the trial ended, too late to influence behavior). SEF activity was therefore inconsistent with a representation of riskiness.

Reward

Another alternative account is that the neuronal activity may be representing upcoming reward amounts for each trial outcome. Neuronal activity levels would map onto actual, rather than expected, reward values for each trial outcome. The prediction would be relatively high firing rates for CH trials and low firing rates for IH trials. As noted above, however, population IH trial activity was greater than IL trial activity and no different than CL trial activity, so reward is not a satisfactory explanation of the neuronal data.

Decision-related signals

Our finding of decision-related signals in the SEF and PFC, in addition to in the FEF (Thompson and Schall, 1999), was interesting but not central to our main result of metacognition-related activity in the SEF. It is important nonetheless to address some potential issues surrounding the interpretation of signals as "decision-related". The masked target task has spatial features that could have introduced confounds. In our analysis of visual-1 and delay activity, we considered only trials in which the target was in the contralateral hemifield. This meant that on Correct trials, the saccade was made into the contralateral hemifield, but on Incorrect trials, the saccade was made into the ipsilateral hemifield. If signals related to preparing the saccade occurred early enough in a trial, they could have mimicked the signals that we interpreted as being correlated with Correct vs. Incorrect decisions. It is well established that saccade preparation/target selection signals are not, in fact, confounded with early visual activity (reviewed by Schall and Thompson, 1999, and Schall, 2001). Early visual responses represent visual stimuli whether they are targets or distractors, and saccadic target selection signals appear when the initial visual response wanes. The differential activity we (and Thompson and Schall, 1999) found that distinguished Correct from Incorrect trials started extremely early in many individual neurons (Figure 2a-c). Even in the averaged population profiles, where latencies of individual visual responses are "smeared" together, it can be seen that the differential responses occurred early. In the FEF and PFC data, in which there was a clear peak to the visual response, Correct-Incorrect differences started prior to that peak (Figure 2a,b). Motor-related signals would not start until well after that peak (Schall and Thompson, 1999; Schall, 2001). Motor-related signals could have contributed to activity in the delay epoch, but even if they did, our main result would be unchanged based on the visual-1 epoch results.

When we analyzed saccade-related activity, we re-sorted trials into those that included only saccades into the contralateral hemifield. This was to explicitly rule out contralateral-ipsilateral differences in activity related to preparation or execution of saccades. In the SEF, we still saw Correct-Incorrect differences, as a

continuation of the signal that started in the visual-1 epoch. The only trivial explanation for those differences would be if SEF neurons had persistent visual responses to briefly flashed, then masked, targets. In that scenario, the higher activity on Correct trials would be attributed to the contralateral target location, and the lower activity on Incorrect trials would be due to the ipsilateral target location. Especially given that SEF visual responses are not prominent to begin with, relative to FEF and PFC visual responses (Figure 2d-f and Figure S2b-d), the idea that the locations of flashed, masked stimuli are represented up to and even after the saccade seems highly unlikely. The most parsimonious interpretation was that the differential activity in the SEF during the presaccadic-1 and postsaccade epochs was correlated simply with making Correct vs. Incorrect decisions.