

1 **Title**

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3 **Macaque dorsal premotor cortex exhibits decision-related**
4 **activity only when specific stimulus-response associations**
5 **are known**

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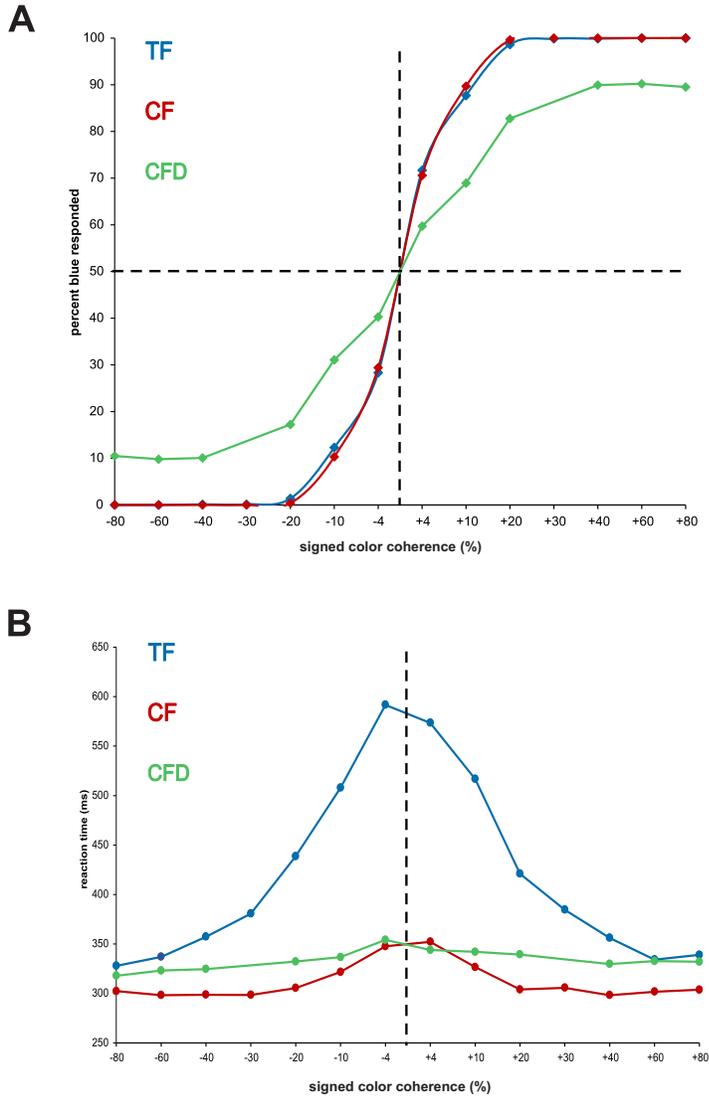
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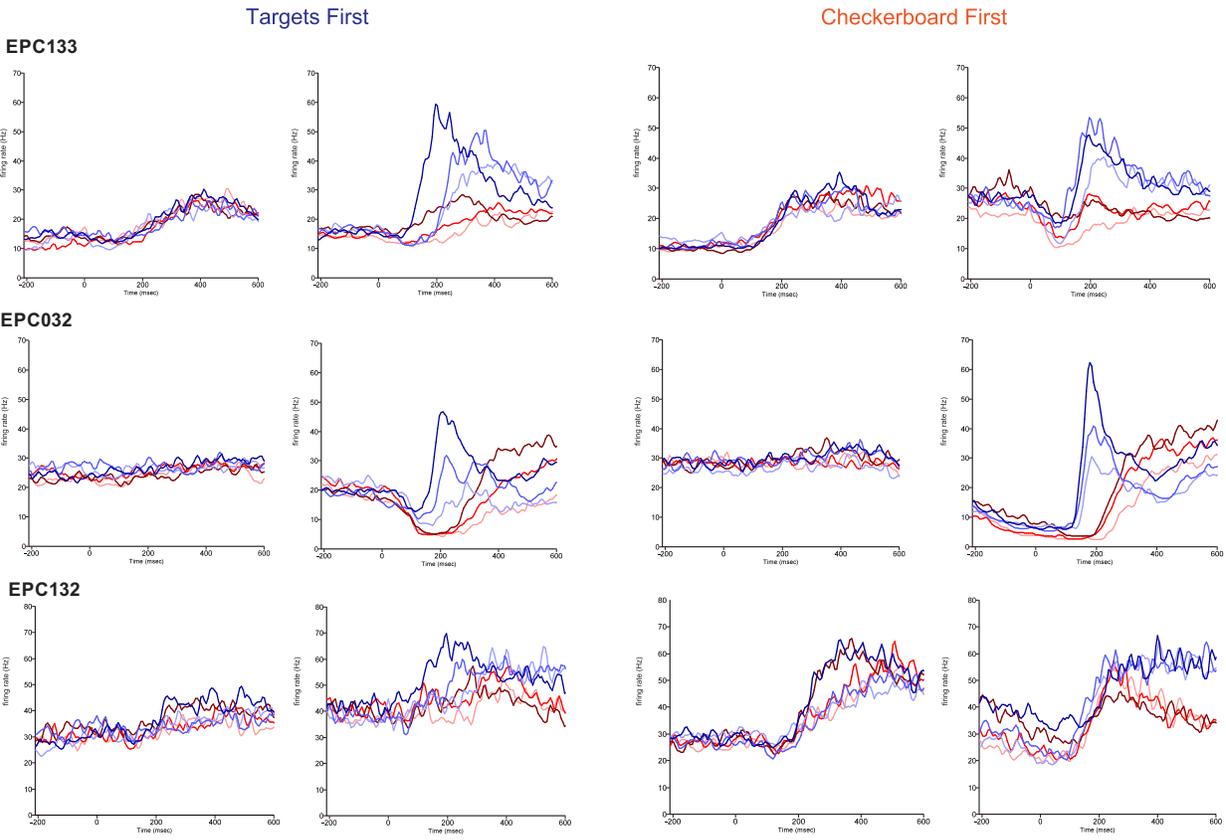
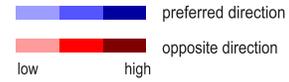
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24 **Supplementary Figures**
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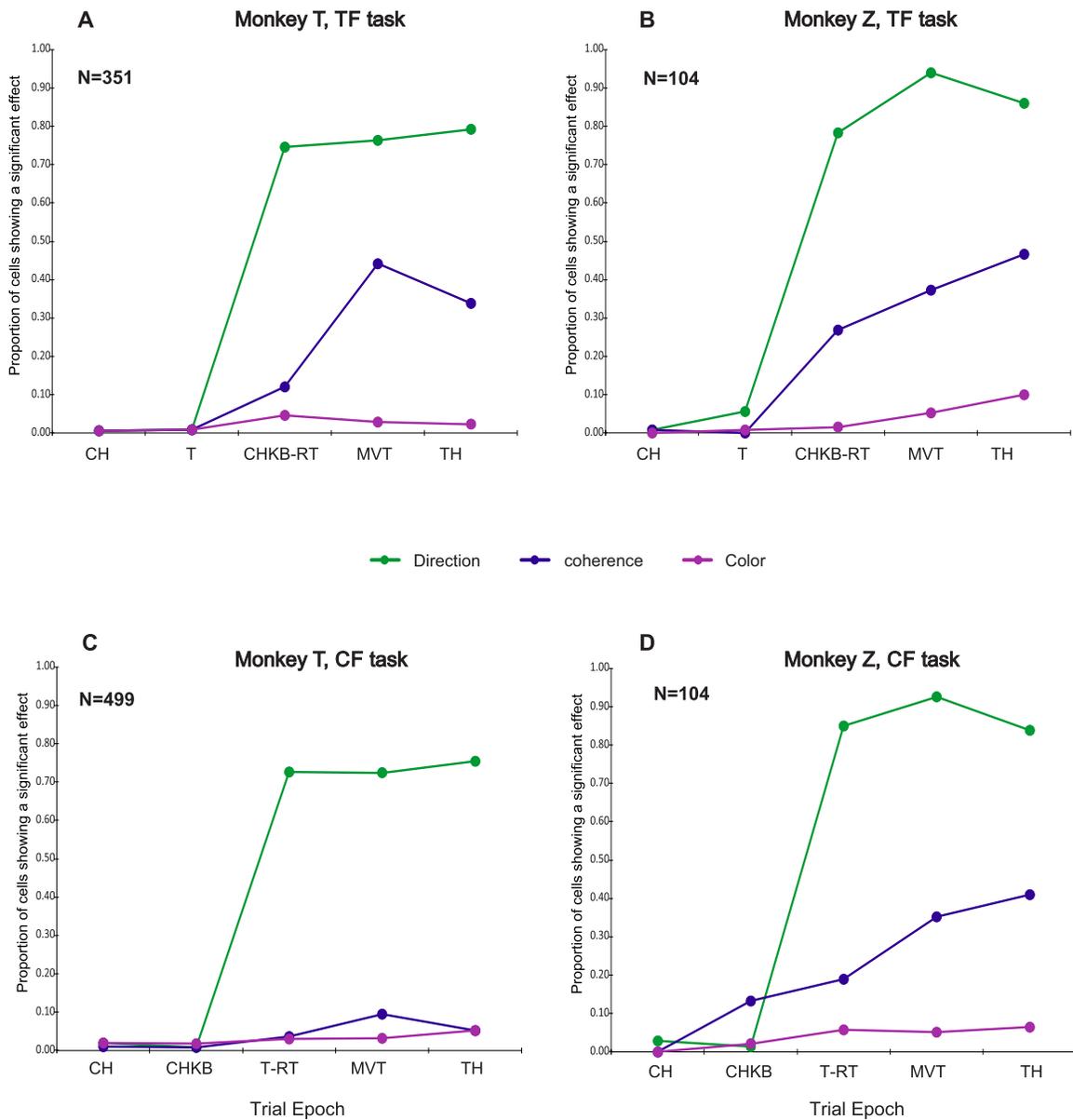
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28 **Supplementary Figure 1.** Monkey Z behavior for all tasks: TF, CF, and CFD. **A)**
29 Psychometric curves and **B)** chronometric curves are shown; compare to Figure 1 **B,C**).
30 TF and CF tasks: same data as in Figure 1 **B,C**. **A)** Like monkey T, monkey Z showed a
31 decrease in success rates for the checkerboards with the highest color coherences in
32 the CFD task compared to the TF and CF tasks. **B)** Unlike monkey T, however, monkey
33 Z continued to show a substantial reduction in RTs for checkerboards with lower color
34 coherences in the CFD task (green line) compared to the TF task (blue line).
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Monkey Z



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Supplementary Figure 2. Further examples of units with responses to first visual cue onset; same format as Figure 3. Unit EPC133 (top) showed a significant rapid response onset (see Methods) at 220ms after the Targets cue appeared in the TF task and 180ms after the Checkerboard appeared in the CF task. Unit EPC032 (middle) did not show a significant rapid response to the Targets in the TF task but showed a late rapid decrease in activity (>600ms) to the Checkerboard in the CF task. Unit EPC132 (bottom) showed a significant rapid increase in response to the Targets at 280ms after they appeared in the TF task, and a significant rapid response increase 220ms after the Checkerboard appeared in the CF task. The response to the Checkerboard was markedly stronger and more rapid for the 100% coherence than for the 20% and 4% coherences. EPC132 showed a significant main effect of evidence Strength in the ANOVA, but did not show a significant linear regression to either the signed color coherence or the signed evidence for reach direction during the Checkerboard-observation period of the CF task.

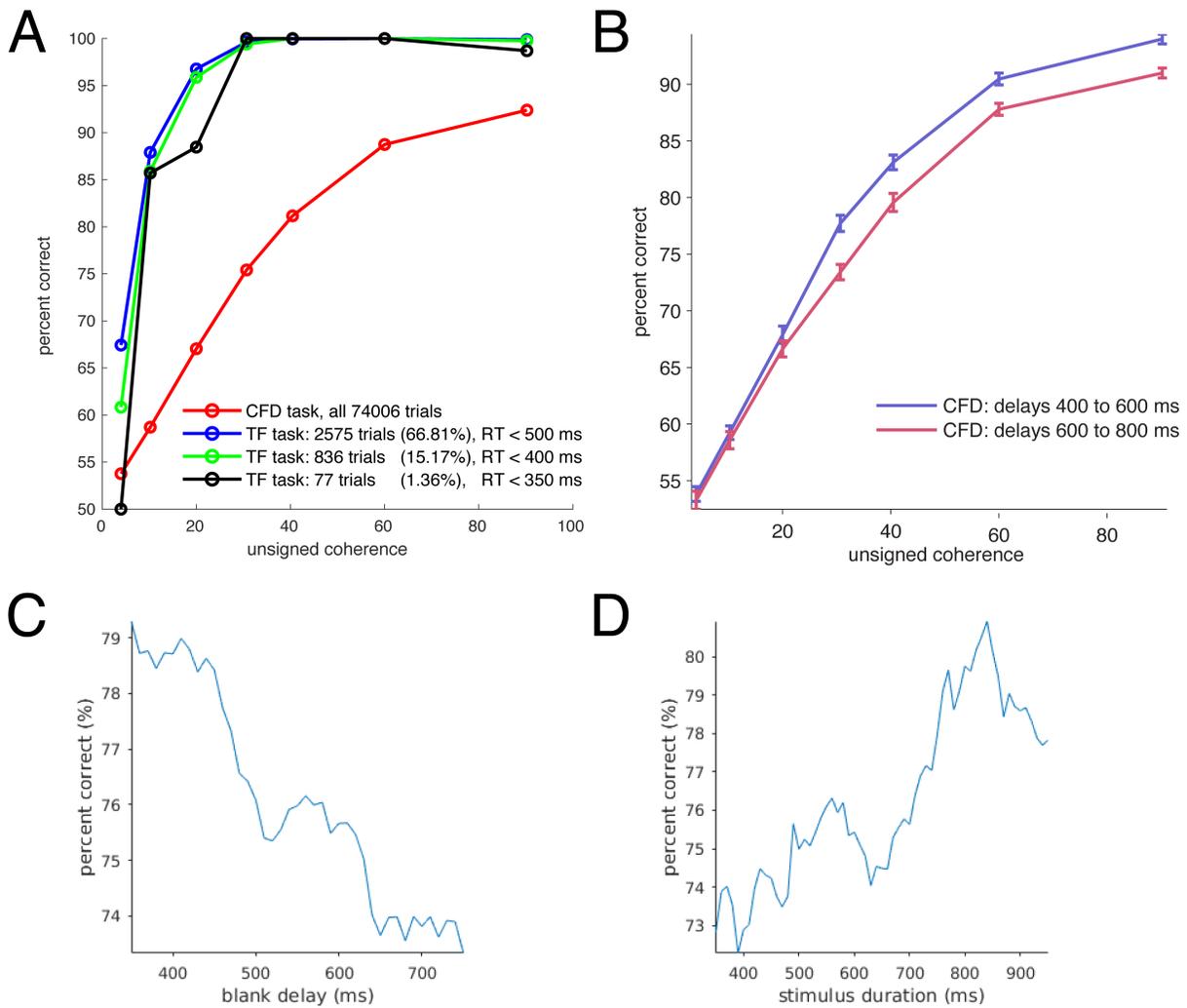


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55 **Supplementary Figure 3.** Proportion of the units that showed a significant main effect
 56 of the task factors chosen reach Direction, unsigned checkerboard evidence Strength
 57 and checkerboard dominant Color in different trial epochs (ANOVA, $p < 0.01$).
 58 **A,B**) TF task. Very few units showed a significant main effect of any task factors during
 59 the Center-hold (CH) and Targets-observation (T) epochs. Furthermore, very few units
 60 in either monkey showed a significant modulation by the color-location conjunction
 61 information provided by the Targets cue during the Targets-observation period
 62 (Direction X Color interaction, $p < 0.01$; Supplemental Table 1). After the checkerboard
 63 appeared, many units in both monkeys showed a significant effect of Direction (green)
 64 during the Checkerboard-RT epoch before the onset of the reaching movements
 65 (CHKB-RT), during the Movement epoch toward the targets (MVT) and during the

66 Target-Hold epoch at the end of the reaching movements (TH). A smaller proportion of
67 units showed a significant main effect of checkerboard evidence Strength (blue) during
68 the CHKB-RT, MVT and TH epochs. Very few units in either monkey showed a
69 significant effect of checkerboard dominant Color (magenta) in any trial epoch. Many
70 units in both monkeys also showed a significant effect of evidence Strength on their
71 Direction responses (significant Direction X Strength interaction, $p < 0.01$). The effects
72 of evidence Strength and the Direction X Strength interaction captured most of the
73 effect of checkerboard coherence on the directional activity of the units in the TF task in
74 all trial epochs after the checkerboard appeared (Figure 2, 3; Supplemental Figure 2).
75 **C,D**) CFD/CF task. Very few units in either monkey showed a significant main effect of
76 Direction during the CH and Checkerboard-observation (CHKB) epochs. Many units
77 emitted strongly Direction signals during the Targets-RT (T-RT), MVT and TH epochs.
78 In monkey T (**C**), relatively few units showed a significant main effect of checkerboard
79 evidence Strength. In contrast, some units in monkey Z (**D**) were significantly modulated
80 by checkerboard Strength during the CHBK epoch, and the number of significant effects
81 of Strength increased progressively during the T-RT, MVT and TH epochs, but fewer
82 than in the TF task. Very few units in either monkey showed a significant effect of
83 checkerboard dominant Color, or Color X Direction or Color X Strength interactions in
84 any trial epoch (see Supplemental Table 1).

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Supplementary Figure 4. Monkey T's behavior as a function of checkerboard duration and blank delay duration.

A) We can compare the performance in the CFD task with performance in the TF task with trials conditioned on reaction time. Since the checkerboard disappears once the hand begins to move, reaction times less than 500 ms mean that the checkerboard viewing time was 500 ms or less in the TF task. Even for reaction times 350 ms or less, the performance is much better than in the CFD task. Thus, the 500 ms checkerboard viewing time in CFD is sufficient to achieve very reasonable discrimination performance.

B) Within all CFD trials, sorting by shorter (400 to 600 ms) and longer (600 to 800 ms) delays reveals that performance is better for shorter delays with a slight sharpening of the slope of the psychometric curve as well as lower lapse rates. Data points are means \pm standard error over sessions.

C,D) To further assess the effect of timing on performance, a subset of 9 sessions explored blank delay durations ranging 300 to 800 ms, and checkerboard stimulus durations ranging 300 to 1000 ms. The percent correct (across all coherences)

104 increases for shorter delays and longer checkerboard durations. These percent correct
105 were calculated in 100 ms bins (e.g. the percent correct for blank delays 300 to 400 ms
106 is plotted at 350 ms) stepping over the range in 10 ms time steps (e.g. the next data
107 point, plotted at 360 ms, calculates percent correct for blank delays 310 to 410 ms).
108

109 **Supplementary Tables**

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111 **A. Targets First task**

Factor		Monkey T (N = 351 units)						Monkey Z (N = 104 units)					
		D	C	S	DxC	DxS	CxS	D	C	S	DxC	DxS	CxS
Center-hold	Units	2	2	2	8	2	3	1	0	1	0	0	2
	Fraction	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.00	0.01	0.00	0.00	0.02
Targets	Units	3	3	3	1	2	0	5	1	0	5	1	1
	Fraction	0.01	0.01	0.01	0.00	0.01	0.00	0.05	0.01	0.00	0.05	0.01	0.01
Checkerboard-RT	Units	260	16	42	7	16	2	79	2	26	5	10	1
	Fraction	0.74	0.05	0.12	0.02	0.05	0.01	0.76	0.02	0.25	0.05	0.10	0.01
Movement	Units	266	10	154	6	61	5	95	7	39	4	19	2
	Fraction	0.76	0.03	0.44	0.02	0.17	0.01	0.91	0.07	0.38	0.04	0.18	0.02
Target-hold	Units	276	8	118	3	57	1	86	10	49	2	20	2
	Fraction	0.79	0.02	0.34	0.01	0.16	0.00	0.83	0.1	0.47	0.02	0.19	0.02

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113 **B. Checkerboard First with Delay / Checkerboard First**

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Factor		Monkey T (N = 499 units)						Monkey Z (N = 104 units)					
		D	C	S	DxC	DxS	CxS	D	C	S	DxC	DxS	CxS
Center-hold	Units	10	10	5	1	5	3	3	0	0	0	2	2
	Fraction	0.02	0.02	0.01	0.00	0.01	0.01	0.03	0.00	0.00	0.00	0.02	0.02
Checkerboard	Units	4	9	4	4	1	5	1	2	12	0	1	0
	Fraction	0.01	0.02	0.01	0.01	0.00	0.01	0.01	0.02	0.12	0.00	0.01	0.00
Targets-RT	Units	360	15	18	17	3	1	88	6	22	4	8	0
	Fraction	0.72	0.03	0.04	0.03	0.01	0.00	0.85	0.06	0.21	0.04	0.08	0.00
Movement	Units	359	16	47	5	15	2	94	6	38	4	18	1
	Fraction	0.72	0.03	0.09	0.01	0.03	0.00	0.90	0.06	0.37	0.04	0.17	0.01
Target-hold	Units	374	26	26	14	17	4	84	7	44	5	15	2
	Fraction	0.75	0.05	0.05	0.03	0.03	0.01	0.81	0.07	0.42	0.05	0.14	0.02

115

116 **Supplementary Table 1.** ANOVA results for monkey T and monkey Z for both tasks: Targets
 117 First (A) and Checkerboard First with Delay / Checkerboard First (B); see Supplementary
 118 Figure 3. D, chosen reach direction; C, checkerboard dominant color; S, unsigned
 119 checkerboard coherence strength; DxC, DxS, CxS, interactions between variables.
 120

121 **Supplementary Discussion**

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123 PMd units in monkey Z but not monkey T exhibited responses to the first sensory
124 information provided in each task

125

126 The response of many PMd units in monkey Z to the appearance of the Target cues in
127 the TF task is consistent with a similar activation of PMd units in a 2-Target memorized-
128 delay task. That activity after the presentation of the two colored target cues has been
129 interpreted as a simultaneous co-activation of two PMd populations that prefer reaches
130 to the two potential targets before a second monochromatic instructional cue identifies
131 the correct target^{1,2}. This activity is sustained during the post-Targets memory-delay
132 period of the 2-Target task, and is a putative neural correlate of a memorized
133 representation of the Target cue information in each trial, expressed in the space of
134 potential actions in PMd (c.f., Horwitz et al³).

135

136 The responses of the units to the appearance of the Checkerboard cues in the CF task
137 likely do not implicate PMd in the perceptual interpretation of the color evidence since
138 the responses were largely insensitive to the salient dimensions (dominant color, signed
139 color coherence) of the stimuli (Figure 5, 6). Alternatively, the activation may reflect a
140 similar process of representation of potential actions as in the TF task. Once a unit in
141 monkey Z was chosen for recording in a given recording session, it was tested with the
142 same two opposite target locations in the task-defined preferred reach direction of the
143 unit and the opposite direction for hundreds of trials in the two tasks. Therefore, it is
144 reasonable to expect that monkey Z had some level of implicit prior knowledge of where
145 the two targets would appear at the start of each trial in both tasks and all that it lacked
146 was the specific color-location conjunction, which it obtained when the targets
147 appeared. The activity during the Checkerboard observation period in the CF task may
148 have reflected the accumulating knowledge of the dominant color of the checkerboard in
149 neural circuits outside of PMd. This may have enabled a covert activation of the
150 simultaneous representations of the two anticipated potential actions even before the
151 targets actually appeared in the CF task since that accumulating sensory evidence will
152 eventually support one or the other of the two colored targets once they appeared. This
153 coactivation of the two PMd populations preferring the two targets may have in turn
154 contributed to the shorter RTs in the CF task than the TF task for even the 100%
155 checkerboards. Critically, however, the linear regression (Figure 5), ROC (Figure 6) and
156 ANOVA (Supplemental Figure 3) showed that these activations during the first-cue
157 observation periods in PMd of monkey Z did not reflect the final decision-related
158 processes as defined here because it did not predict any aspect of monkey Z's
159 differential choice behavior after the second visual cue appeared in each task.

160

161 Since activation of PMd by partial action-related information before the final action
162 choice can be specified is a robust finding in several different studies^{1,2,4-15}, why did
163 monkey T not show any activity in PMd during the first visual-cue observation periods in
164 the TF and CFD tasks? This could occur if different cortical regions were sampled in

165 monkeys T and Z. Both monkeys are still participating in neural recordings and
166 histological localization of penetration sites has not yet been done. However, similar
167 stereotactic coordinates for chamber implants and extensive relative overlap of
168 recording penetrations within the chambers in the two monkeys suggest that is not the
169 main cause (Figure 1E).

170
171 Another possible explanation is the different training history of the two monkeys.
172 Monkey T only ever experienced L/R targets and was initially trained in the TF task in
173 which the targets remained visible for the duration of each trial. Thus, its original training
174 experience did not require the establishment of a memorized trace of the target
175 information. In contrast, monkey Z was trained for many months in the 1T and 2T tasks
176 with targets in 8 different directions that varied from trial to trial and with two long
177 sequential memory-delay periods during which the monkey had to remember the spatial
178 location (1T task) and color-location conjunctions of the targets in each trial before
179 selecting a target (2T task), and initiating a reach (1T and 2T tasks). The 1T and 2T
180 tasks were also used in all neural recording sessions to search for task-related units.
181 Engagement of PMd during the memory-delay periods of the 1T and 2T tasks may have
182 facilitated task performance for monkey Z, which was carried over to the TF and CF
183 tasks.

184
185 Another possible contributing factor is the target location placement in the tasks. For
186 monkey Z, targets were placed in spatial locations along the preferred-opposite
187 movement direction axis of each unit to maximize the difference in their directional
188 activity in the TF and CF tasks, and would change from unit to unit. For monkey T, in
189 contrast, target locations were fixed to the left and right of center, and units were
190 recorded for that single movement axis, regardless of what their preferred reach
191 directions might have been.

192
193 Finally, the lack versus presence of activity changes after the checkerboards appeared
194 in the CF/CFD tasks may have reflected a difference in the strategy that the two
195 monkeys adopted to perform the tasks. Monkey T may have adopted a strategy
196 whereby it attempted to store a purely “sensory” mnemonic representation of the
197 checkerboard stimuli but largely deferred the interpretation of the checkerboard
198 evidence until the appearance of the targets. This resulted in no PMd responses and
199 longer RTs in the CFD task compared to the TF task. In contrast, monkey Z appeared to
200 largely commit to a categorical decision about the dominant color of the checkerboard
201 while observing it in the CF task, resulting in a substantial reduction in RTs after the
202 targets appeared. This may have been accompanied by a covert activation of the two
203 competing action-related PMd populations, like in the TF task, while monkey Z
204 deliberated on the color evidence in the checkerboard, even though the targets had not
205 yet appeared. This is further reinforced by the finding that monkey Z’s RTs remained
206 drastically shorter in a modified version of the CF task that had the same temporal
207 structure as the CFD task. This showed that monkey T’s prolonged RTs in the CFD task
208 compared to the TF task were not due solely to the imposed memory-delay period but

209 rather to how and when it interpreted that task-relevant sensory evidence provided by
210 the checkerboards.

211
212 How did the monkeys convert checkerboard color coherence into reach actions?

213
214 The systematic differences in the rate of rise of reach-related directional signals in PMd
215 as a function of the color coherence of the checkerboards in the TF task are reminiscent
216 of similar correlations with the coherent motion strength of RDK stimuli seen in saccade-
217 related cortical regions¹⁶⁻¹⁸ and in parietal cortex area 5 in an arm reach task¹⁹. Those
218 findings have been interpreted as the neural correlate of a process of accumulation of
219 noisy sensory evidence across time using signals generated by motion-sensitive
220 neurons in medial temporal cortex (MT) to inform the choice of the action that must be
221 performed to report a decision about perceived net motion direction. This makes
222 intuitive sense since the RDK stimuli are stochastic, contain variable amounts of dot
223 motion in random directions as well as in the coherent motion direction from moment to
224 moment, and only evoke reliable sensations of coherent visual motion in a particular
225 direction when experienced over time¹⁷.

226
227 In contrast, the checkerboards used in these tasks comprised sets of small squares
228 whose colors are easily and rapidly discriminable, and contained no input signal “noise”
229 comparable to the variable numbers of dots moving in the coherent and random
230 directions from frame to frame in the RDK stimuli. The checkerboard stimuli presented
231 in half of the trials to monkey Z were dynamic and changed every 50ms, but the
232 numbers of blue and yellow squares in each stimulus stream remained fixed in a given
233 trial and only their positions within the checkerboard changed from image frame to
234 image frame. In contrast, in the other half of the trials for monkey Z and all of the trials
235 for monkey T, a single static checkerboard of R/G or B/Y squares appeared for the
236 duration of the observation period in each trial, so that the physical properties of the
237 sensory stimulus that the monkeys experienced did not change across time. Despite
238 these differences in the visual stimuli, the two monkeys showed remarkably similar
239 chronometric and psychophysical trends in the TF task (present study; ²⁰). Furthermore,
240 human and non-human subjects also showed very similar performance when viewing
241 either dynamic or static checkerboard stimuli (^{2,21}; present study). Thus, whereas the
242 motion sensations evoked by RDK stimuli require dynamically changing stimuli across
243 time, the assessment of the color evidence in the checkerboards was relatively
244 insensitive to the presence or absence of continually updated sensory inputs. This does
245 not, however, preclude momentary stochastic noise generated within the central neural
246 circuits that process even the static checkerboard visual input (both monkeys) and store
247 it in short-term working memory (monkey T).

248
249 The similarity of task performance in the TF task is also striking given another difference
250 in the checkerboard stimuli experienced by the two monkeys. The checkerboards used
251 in monkey T’s experiments contained only task-salient R and G squares. In contrast, the
252 checkerboards used in monkey Z’s experiments contained 100 task-salient B and Y

253 squares against a background of 125 task-irrelevant R squares. This reduced the
254 overall density of task-relevant color information in the checkerboards for monkey Z and
255 required it to identify the task-relevant information from among the “distractor” red
256 squares. Despite this difference, the psychophysical curves and psychophysical
257 thresholds of the two monkeys were very similar in the TF task, and the RTs for the
258 high-coherence checkerboards were actually shorter in monkey Z than monkey T
259 (Figure 1).

260
261 Despite the absence of color evidence “noise” in the checkerboards and the insensitivity
262 of task performance to static versus dynamic stimuli, the monkeys took longer to choose
263 a colored target when the checkerboard coherence decreased^{2,20,21}. In RDK stimuli, this
264 effect has been explained by a sequential-sampling process that takes longer to identify
265 the direction of the weak coherent-motion signal generated by MT neurons against a
266 high level of motion direction noise. For the checkerboard stimuli, in contrast, it
267 presumably reflects a longer period of time required to determine whether the
268 checkerboard was predominantly one or the other of the two task-salient colors as the
269 numbers of squares of the two easily-discriminable colors became more similar. This
270 may require longer re-sampling of the sensory input while observing the checkerboard
271 (monkey Z) or from a noisy working-memory trace of the checkerboard (monkey T; ^{22,23},
272 Shushruth and Shadlen, CoSyNe abstract). We can assume that the color evidence is
273 initially processed by neurons in the parvocellular “color-opponent” pathway²⁴⁻²⁷.
274 However, to our knowledge, there have been no studies of neural responses in that
275 pathway to multi-colored checkerboard stimuli like ours in color discrimination tasks
276 analogous to the many studies of visual motion processing in MT.

277
278 The perceptual decision could be considered as a pure color discrimination problem
279 since the subjects had to estimate the dominant color of the checkerboards in order to
280 identify the reach target whose color matched that of the checkerboard. However,
281 similar dichromatic dot arrays have been used in studies of numerosity, the ability of
282 subjects to estimate relative numbers of visual objects²⁸⁻³⁰. Subjects likewise showed
283 longer RTs when the relative numbers of objects in the stimuli are similar^{30,31}. These
284 results have been interpreted as consistent with a process of sequential sampling and
285 accumulation of evidence across time and across space within the stimuli³⁰⁻³³, but did
286 not speculate on the nature of the sensory evidence that was being sampled, unlike
287 RDK stimuli. Furthermore, the checkerboards that we used have inherent in them
288 several potential confounding “low level” physical properties identified in numerosity
289 studies that are independent of the presumably “higher level” sense of relative numbers
290 per se, including the relative area of the checkerboard occupied by squares of each
291 color, their total circumference, and the relative degree of spatial contiguity of squares
292 of the same color (i.e., how often they cluster to share a common border)^{30,34-37}. Indeed,
293 the colored squares did not have a neutral-colored border and so would form larger
294 monochromatic “clumps” when contiguous, rather than remaining visible as discrete
295 squares (Figure 1D). All of these factors could have contributed to the monkeys’
296 estimation of the dominant color of the checkerboards, independent of any estimate of

297 relative numbers of squares. Furthermore, the number and density of squares in our
298 checkerboards were usually higher than normally used in numerosity studies and more
299 closely resemble what are called “textures”, which follow different psychophysical laws
300 than dot arrays with smaller numbers of elements²⁸.

301
302 However, this study was not designed to study numerosity or to examine what specific
303 properties of the checkerboards the subjects used to make the relative color estimates.
304 Instead, the checkerboards were chosen as a means to present stimuli with different
305 levels of competing evidence for two alternative reach choices, using a stimulus
306 dimension (color) that has no inherent natural association with the directionality of motor
307 output. Our findings indicate that PMd units express activity pertaining to the likelihood
308 of different action choices provided by the checkerboard stimuli, independent of the
309 critical decision-relevant physical property of the sensory input on which those action
310 likelihoods are based, in this case its dominant color.

311
312 Important questions not directly addressed by this study are where are the neural
313 correlates of the critical color-related information on which the action decisions were
314 based and how are they transformed into color-independent evidence supporting the
315 action choices? A strong candidate is the dorsolateral prefrontal cortex^{38,39}. We have
316 preliminary evidence that the specific color/location conjunctions of the spatial target
317 cues and color/location matching rules after the checkerboard appeared in each trial are
318 expressed in lateral prefrontal cortex around the principal sulcus while a monkey
319 performed a TF task (Coallier et al., 2008, SfN abstract).

320
321 The effect of checkerboard color coherence on task performance and PMd neural
322 activity is consistent with a number of different computational decision-making models,
323 including drift-diffusion^{17,18,30,40,41}; gated stochastic accumulation^{42,43}, urgency
324 gating^{44,45}, and independent-race⁴⁶⁻⁴⁸. Nevertheless, we acknowledge that our neural
325 data are correlational and are not proof of a causal relationship between PMd activity
326 and either perceptual or motor decisions. Furthermore, until more neurophysiological
327 findings are available about the sources and nature of sensory signals that are being
328 processed while subjects estimate the relative amounts of colored squares in the
329 dichromatic checkerboard stimuli, and how those sensory signals are transformed into
330 action-related information, we prefer to remain agnostic as to the computational
331 mechanisms that underlie the task performance of the subjects.

332 **Supplementary References**

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