

1 **A causal role for the posterior corpus callosum in bimanual** 2 **coordination**

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18 Main Text

19 Figures 1 to 4

20 Supplemental Information

21 **Abstract**

22 Inter-areal communication is crucial for brain function. Given the largely contralateral
23 organization of the brain, bimanual coordination likely involves interactions across the
24 two cerebral hemispheres for motor planning and execution. The parietal reach region
25 (PRR) is an early node in the sensorimotor transformation stream. Here we examine the
26 contributions of direct callosal connections between left and right PRR to bimanual
27 coordination. Using manganese-enhanced magnetic resonance imaging, we traced
28 callosal pathways crossing the midline and found that PRR-PRR connections are
29 restricted to the splenium. We then temporarily blocked these fibers with lidocaine while
30 measuring behavioral performance and interhemispheric coherence. Blockade reduced
31 task-specific PRR-PRR coherence during bimanual movements. Behaviorally, blockade
32 sped movement initiation across tasks, consistent with an inhibitory role of
33 interhemispheric communication, reduced the temporal synchrony of bimanual
34 movements to a common target and reduced errors for bimanual movements to separate
35 targets. These findings provide causal evidence that posterior callosal communication
36 supports spatial coordination of bimanual actions but may also constrain independent
37 limb control.

38 **Significance Statement**

39 Classic split-brain studies revealed that severing the corpus callosum impairs bimanual
40 coordination, but the specific pathways and mechanisms remain unclear. In macaques,
41 we transiently disrupted the posterior corpus callosum connecting left and right parietal
42 reach regions (PRR), which encode planned contralateral arm movements. This targeted
43 blockade reduced task-specific neural synchrony between PRRs and selectively
44 impaired coordination when both arms reached to a common target, while improving
45 performance when the arms moved to separate targets. Movement initiation was also
46 sped up across tasks, consistent with an inhibitory role of interhemispheric
47 communication. These findings provide causal evidence that posterior callosal
48 communication enables spatially coordinated bimanual movements, extending
49 foundational split-brain insights to defined cortical circuits in a non-human primate
50 model.

51 **Introduction**

52 Primates excel at planning and coordinating movements (1–4). Tasks that appear to be
53 accomplished using a sequence of independent sensory-to-motor transformations may
54 in fact require advance movement planning and coordination of different body parts (5–
55 9). Scaling a cliff, for example, requires a series of coordinated limb movements to select
56 optimal handholds for ascent. Many steps involve coordinated movements of all four
57 limbs at once, shifting weight and bracing as one reaches to grasp the next hold. Such
58 tasks emphasize the importance of interlimb coordination (10, 11).

59 Each cerebral hemisphere primarily controls the contralateral limbs (12–17). Given the
60 largely lateralized organization of the brain, bimanual coordination likely requires
61 interactions across the cerebral hemispheres (18–22). Reach planning and execution
62 drives systematic patterns of activity in the functionally defined parietal reach region
63 (PRR) of the posterior parietal cortex (23–27). The population average firing rate in PRR
64 specifically codes planned reaches of the contralateral arm (23, 25, 26), and lesions in
65 PRR impact these movements (14, 28–31). However, beta-band local field potential (LFP)
66 power, reflecting both areal input and local processing (32–34), carries information about
67 both arms (35). Thus, while PRR output primarily encodes contralateral arm information,
68 it receives information about the ipsilateral limb from other areas, perhaps including PRR
69 in the opposite hemisphere (35).

70 Bimanual tasks provide a means to study how the cerebral hemispheres interact to
71 coordinate the movements of two limbs (36–41). Bilateral recordings made in PRR during
72 bimanual reaching tasks show that interhemispheric LFP-LFP and spike-LFP coherence
73 is modulated by movement type (35). This shared information could arise either from
74 common input to, or from direct communication between left and right PRR.

75 The corpus callosum is the principal path for information flow between the two cerebral
76 hemispheres (42–44). Gross sectioning of the anterior, posterior, or the whole corpus
77 callosum in humans degrades bimanual coordination (45–48). Yet there is little
78 consensus about how specific callosal pathways support information exchange and
79 complex behaviors (42, 44, 49–51).

80 Here, we identified and transiently blocked callosal fibers connecting left and right PRR
81 to examine their role in coordinated bimanual behavior. Callosal communication appears
82 to support symmetrical movements to a single target and effectively impedes
83 asymmetrical movements to different targets, consistent with previous clinical studies
84 with callosotomy patients (45–47). Additionally, the modulation of interhemispheric LFP-
85 LFP coherence between left and right PRR based on bimanual movement tasks was
86 significantly reduced during blockade. These results support a causal role of direct
87 interhemispheric communication between left and right PRR in bimanual coordination.

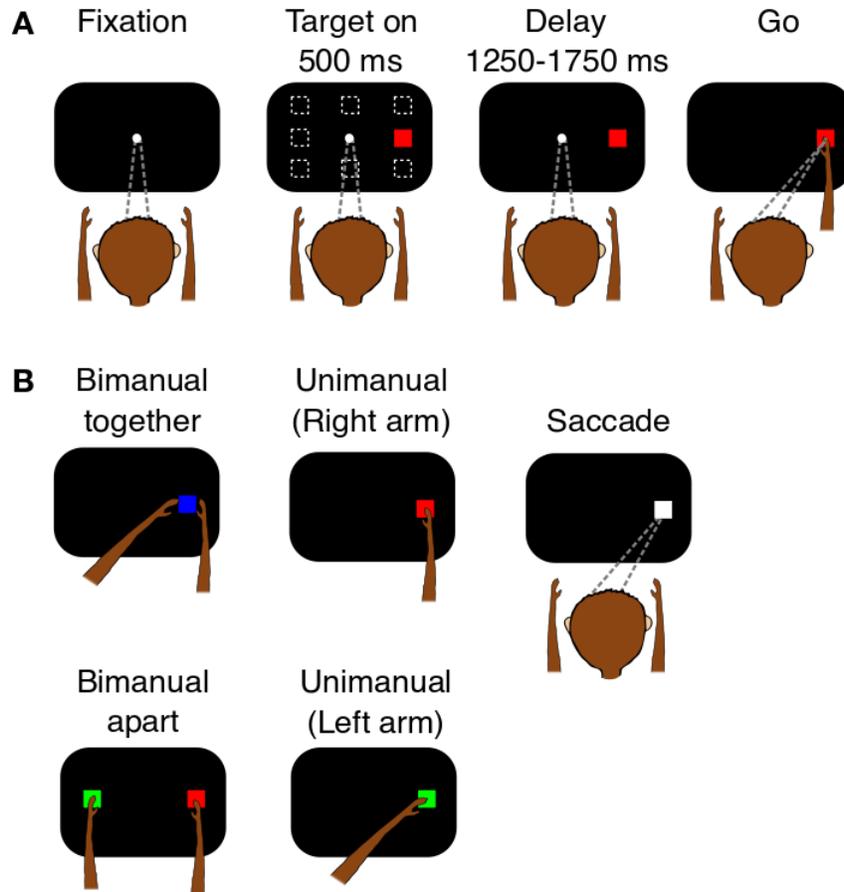
88 **Results**

89 To establish a baseline, we recorded activity in PRR while animals planned different
90 types of control and coordinated movements (saccades, ipsimanual reaches,
91 contramanual arm reaches, bimanual reaches to the same target, and bimanual reaches
92 to two different targets [Fig. 1]). We identified index cells as single units on the medial
93 bank of the intraparietal sulcus, close to the junction with the parieto-occipital sulcus,
94 that showed strong delay period activity for reaches. We defined PRR as the region
95 spanned by these index cells and classified all task-responsive cells lying within 2 mm
96 of the index cells as PRR cells, regardless of their activity patterns. The population of all
97 such recorded single units shows three levels of delay period activity, similar to
98 previously published results (26). Activity is high when the goal lies in the preferred
99 direction (“preferred”) and when the movement plan includes a reach with the
100 contralateral arm (e.g., a contramanual reach or a coordinated bimanual reach to a single
101 target). Activity is low for any movement away from the preferred direction (“null”).
102 Finally, activity is intermediate when the goal lies in the preferred direction and the
103 movement plan does not include a contramanual reach (i.e., a saccade or ipsimanual
104 reach). Thus, at the population level, PRR neurons distinguish the direction of a planned
105 movement and, for movements in the preferred direction, whether that plan includes a
106 reach with the contramanual arm. In contrast, beta-band LFP power does not distinguish
107 movement direction but does distinguish each of the five movement types described
108 above (Fig. S1A–B; see also Mooshagian et al., 2021) (35). Results from the first animal
109 have been previously reported (Monkey T) (26, 35, 52–54), while results from the second
110 animal replicate that work (Monkey J).

111 The action potentials from single units are directional but LFP is not. PRR, unlike many
112 other posterior areas, contains roughly equal numbers of intermingled cells with
113 contralateral or ipsilateral response fields (RFs) (26, 55). An LFP recording combines
114 (dendritic, somatic, and axonal) signals from many cells, and therefore directional
115 specificity is lost. However, the fact that LFP retains sensitivity to the five types of
116 movements is not so easily explained. Mooshagian and colleagues proposed that each
117 PRR codes reach plans for just the contralateral arm (35). Cells from the opposite PRR
118 provide information about what the other arm (the ipsilateral arm) is doing, allowing PRR
119 to adjust the contralateral arm plans, thereby providing a neuronal mechanism for
120 bimanual coordination. A simple model shows that this can explain the levels of LFP
121 activity seen in PRR (Supplementary Fig. 13 of Mooshagian et al., 2021) (35).

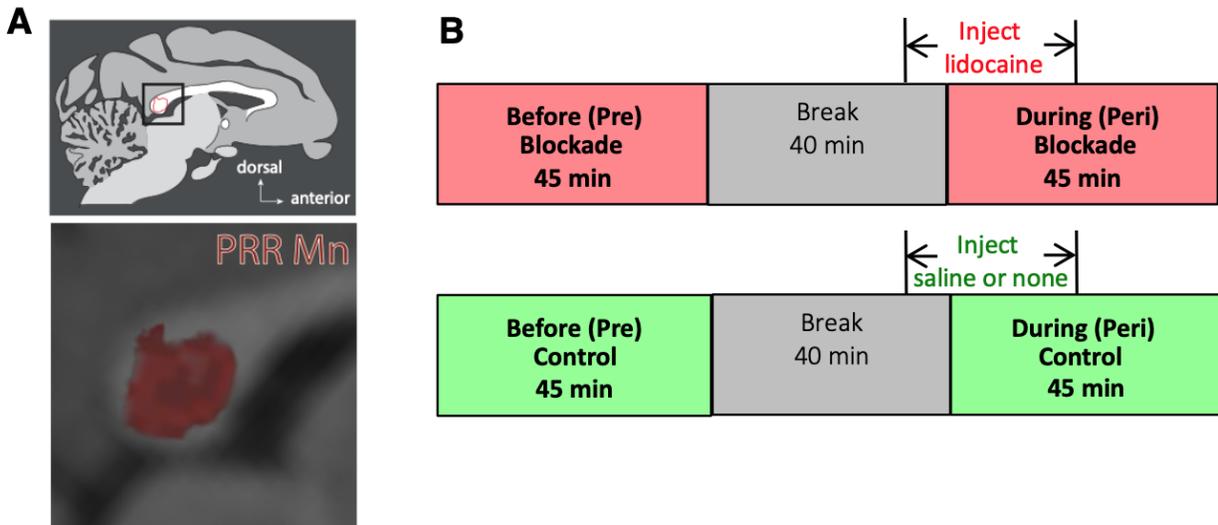
122 To examine the role of callosal connections between left and right PRR in bimanual
123 coordination, we recorded spikes and LFPs in both hemispheres simultaneously and
124 compared reaching behavior and neuronal activity before and during blockade of
125 homotopic callosal connections between left and right PRR. To identify the relevant
126 pathways, we injected manganese into PRR and then used *in vivo* manganese-enhanced
127 magnetic resonance imaging (Mn-MRI) to trace white-matter pathways between PRR in
128 each hemisphere (56, 57). Axons from PRR crossing to the opposite hemisphere in the
129 posterior portion of the brain were restricted to the splenium (Fig. 2A and Fig. S2A). We
130 reversibly blocked these callosal pathways by injecting 5 μ L of a 2% lidocaine solution
131 into the splenium at a rate of 0.15 μ L/minute. We confirmed our targeting by co-injecting
132 manganese with the lidocaine and imaging the animal to confirm that we had injected
133 the same area that we had identified in the tract-tracing experiments (Fig. S2B–C).

134 We obtained two blocks of 400-480 interleaved trials of the five delayed movement tasks
135 (Fig. 2B). One block (Pre) was collected before the injection and a second block (Peri)
136 began once 1.0 μ L of lidocaine was injected and ended within 20 minutes after the end
137 of the injection. We also ran control sessions in which a guide tube was lowered and
138 either saline or nothing was injected. We compared behavioral performance and neural
139 activity between callosal blockade and control sessions.



140 **Fig. 1.** Delayed movement tasks.

141 (A) Delayed movement tasks. Animals first fixated on a central target and placed each
142 hand on a home button situated at waist height in front of each shoulder. After an initial
143 fixation period of 500 ms, a peripheral target appeared at one of eight possible peripheral
144 positions (dotted squares). The color and location of the target instructed a particular
145 movement. The target remained visible throughout a variable delay period (1250-1750
146 ms). After the delay, the disappearance of the fixation target cued the animal to perform
147 the instructed movement. Reproduced from Kang et al. (2024), *Cell Reports*, under CC
148 BY-NC license (54). (B) Types of movement tasks. Animals performed two types of
149 bimanual movements: “Bimanual-together” (two arms, one target) and “Bimanual-apart”
150 (two arms, two targets). Bimanual-together movements were both spatially and
151 temporally coordinated, that is, directed towards the same target, whereas bimanual-
152 apart movements were not spatially coordinated (different targets). Unimanual reaches
153 and saccade-only trials served as controls.

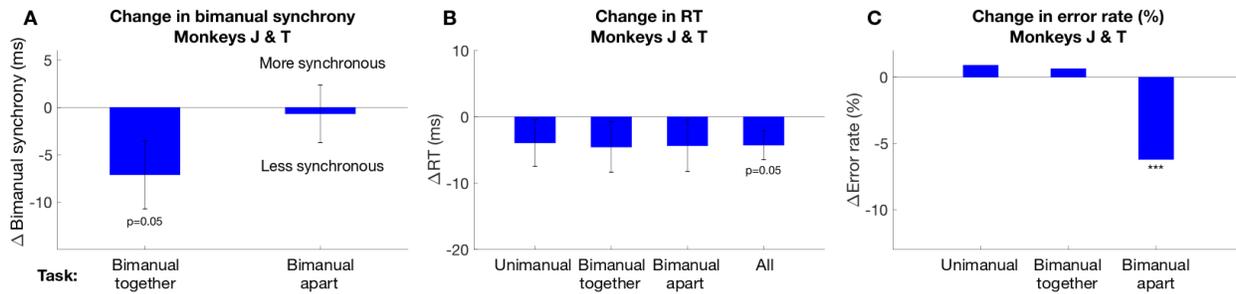


154 **Fig. 2.** Experimental design.

155 (A) Localization of callosal fibers connecting left and right PRR using Mn-MRI. Top,
156 callosal fibers projecting from right PRR and through the corpus callosum were restricted
157 to the splenium (red outline). Bottom, an expanded view. Full Mn-MRI scan showing the
158 anterograde transport of Mn from PRR is in Fig. S2. (B) Timeline of experimental and
159 control sessions. Each session comprised two blocks of 400 or 480 trials each. One
160 block was completed before (Pre Blockade) and one during (Peri Blockade) the injection
161 with a 40-minute break between the two. Experimental and control sessions differed by
162 whether a real or sham injection was conducted. In experimental sessions, lidocaine was
163 injected (5.0 μL for Monkey J and 5.5 μL for Monkey T of 2% lidocaine solution; rate =
164 0.15 $\mu\text{L}/\text{minute}$). In control sessions, either saline or nothing was injected. Peri Blockade
165 blocks began once 1.0 μL of lidocaine was injected (6.6 minutes) and ended 15 minutes
166 after the injection was completed (see Methods).

167 **Callosal pathways facilitate temporal synchronization and spatial coordination of**
168 **bimanual movements**

169 We first tested whether posterior callosal pathways might help synchronize movements
170 of the two arms. We quantified bimanual synchrony by measuring the absolute difference
171 in reaction times (RTs) between the two arms, with smaller differences indicating greater
172 synchrony. Fig. 3A shows how synchrony changes with callosal blockade for the two
173 bimanual movement tasks. Upward (positive-going) bars indicate an increase in
174 synchrony. During callosal blockade, bimanual-together movements became less
175 synchronous by -7.1 ± 3.6 ms (pooled t-test, $p = 0.054$, both animals; -7.3 ms \pm 4.3 ms,
176 Monkey J and -5.1 ms \pm 5.2 ms, Monkey T; Fig. S3A and Fig. S3D). Critically, blockade
177 had no effect on the synchrony of bimanual apart movements (-0.7 ± 3.0 ms; pooled t-
178 test, $p = 0.824$). A non-specific effect of blockade on movement timing would degrade
179 the synchrony of both types of movements. These results are therefore consistent with
180 callosal pathways helping to synchronize spatially coordinated movements of the two
181 arms to a single target.



182 **Fig. 3.** Behavioral performance in callosal blockade and control sessions.
183 (A) Change in bimanual synchrony as a function of bimanual movement type and session.
184 We assayed the effect of callosal blockade on the absolute reaction time difference
185 between the two arms, $\Delta(|RT_{\text{Left}} - RT_{\text{Right}}|)$ in Peri minus Pre blocks. We compared the
186 change in bimanual synchrony from Pre to Peri blocks in control ($n = 24$) and blockade
187 ($n = 22$) sessions. Positive-going values indicate higher bimanual synchrony during
188 callosal blockade than in control sessions. In bimanual-together movements, we
189 observed significantly less synchronous bimanual movements in blockade sessions
190 compared to control sessions ($p = 0.05$, pooled t-test). No significant changes were
191 observed in bimanual-apart trials. (B) Change in RT. Callosal blockade sped movement
192 initiation (shorter RTs) compared to control for all three movement types. This speeding
193 effect was statistically significant when averaged across all movement types ($p = 0.05$,
194 pooled t-test). ΔRT (Peri - Pre) is calculated as the difference between the median RT in
195 the Peri block and the median RT in the Pre block for each movement type (Unimanual,
196 Bimanual-together, Bimanual-apart) in control versus callosal blockade sessions. Error
197 bars in (A) and (B) denote the standard error of the mean (SEM). Changes in bimanual
198 synchrony and RT in control and blockade sessions are shown separately in Fig. S4. (C)
199 Change in error rate. Callosal blockade improved bimanual-apart movements compared
200 to control ($p < 0.001$, logistic regression). Δ Error rate (Peri - Pre) is calculated as the
201 difference between error rates in the Peri block and Pre block. Error rate in each block
202 is calculated from data concatenated across all sessions. We compared the change in
203 error rates in control and blockade sessions. We performed logistic regression with block
204 (Pre, Peri) and condition (Control, Blockade) as two factors, and show the statistical
205 significance of the interaction term of the two factors. *** $p < 0.001$

206 Next, we considered the mechanism by which callosal communication helps
207 synchronize the two arms. We hypothesized that callosal pathways either slow down the
208 faster arm or speed up the slower arm to achieve temporal coordination. Compared to
209 control sessions, callosal blockade resulted in faster RTs across all tasks, including
210 unimanual reaches (Fig. 3B). When pooled across tasks, the effect was significant (-4.3
211 $\text{ms} \pm 2.2 \text{ ms}$, pooled t-test, $p = 0.05$). This effect was present in both animals, but
212 reached significance only in Monkey J ($-7.8 \text{ ms} \pm 3.2 \text{ ms}$, $p = 0.016$, pooled t-test; Fig.
213 S3B). In Monkey T, the effect trended towards faster RTs in a reaction time task in which
214 the animal could move as soon as the target appeared ($-9.0 \pm 6.1 \text{ ms}$, $p = 0.149$, pooled
215 t-test; $n=10$ blockade sessions, $n=10$ control sessions; only Monkey T performed this
216 task). Thus, blocking callosal transmission speeds up reaching movements. For spatially
217 coordinated movements (bimanual-together), RTs became faster but less synchronous.
218 For spatially distinct movements (bimanual-apart), RTs also became faster but without
219 significant changes in synchrony. These results indicate that callosal communication
220 supports bimanual temporal coordination by slowing down the faster arm rather than
221 speeding up the slower arm.

222 We also assessed effects of blockade on spatial accuracy. We used capacitive proximity
223 sensors rather than a touch screen or similar device to sense multiple independent
224 touches. As a result, we do not have precise estimates of spatial endpoints. However,
225 we know from monitoring reaches on real time video that almost all arm-related errors
226 occurring after the go cue resulted from the animal landing off-center on the correct
227 capacitive switch, and not because the wrong button was targeted (see Methods and
228 Table S1 for details). As a result, the rate of arm errors occurring after the go cue provides
229 a proxy for reach accuracy. Blockade improved accuracy for bimanual-apart movements
230 ($p < 0.001$, logistic regression) and did not affect unimanual and bimanual-together

231 movements. When separated by animal, the bimanual-apart effect was significant in
232 Monkey T, who also showed a significant improvement in bimanual-together movements
233 ($p < 0.01$, logistic regression; Fig. S3F). Monkey J showed non-significant improvements
234 in both types of bimanual movements (Fig. S3C). Taken together, the effects on
235 synchrony and spatial accuracy suggest that callosal communication helps yoke the two
236 arms together and interferes with bimanual movements to different targets, such that
237 blocking the callosum impairs bimanual-together movements and improves bimanual-
238 apart movements. This is reminiscent of results from patients with posterior callosotomy,
239 in whom symmetric arm movements are impaired while asymmetric movements are
240 improved (45, 47).

241 We performed similar analyses on synchrony, RT, and error rates as a function of
242 laterality and symmetry (see Methods and Fig. S5). Movements were categorized as
243 crossed or uncrossed based on the neuroanatomical relationship between the stimulus
244 and movement. In crossed movements, each arm reached to a target in the contralateral
245 visual hemifield, meaning that the hemisphere that processed the spatial location and
246 one that controls the movement were different, requiring interhemispheric transfer. In
247 uncrossed movements, the stimulus and motor planning the stimulus and the motor
248 planning occurred in the same hemisphere, and therefore did not require
249 interhemispheric transfer. Movements were categorized as symmetric or asymmetric
250 based on whether the arms moved in a spatially mirror-symmetric fashion (e.g., toward
251 mirror opposed targets) or toward the same lateralized target. Compared to control
252 sessions, callosal blockade sessions resulted in reduced synchrony during asymmetric
253 movements (Fig. S6), no significant change in RT (Fig. S7), and fewer errors in crossed
254 movements (Fig. S8). The observed reduction in synchrony for asymmetric movements
255 is consistent with the notion that callosal communication facilitates temporal

256 synchronization of bimanual asymmetric movements to a single target in either visual
257 hemifield. Fewer errors in crossed bimanual movements during callosal blockade
258 indicate that intact callosal communication may be disruptive for bimanual coordination
259 when each arm moves to a target in the contralateral visual hemifield.

260 **Callosal blockade greatly reduces task-specific modulation of interhemispheric**
261 **LFP-LFP coherence**

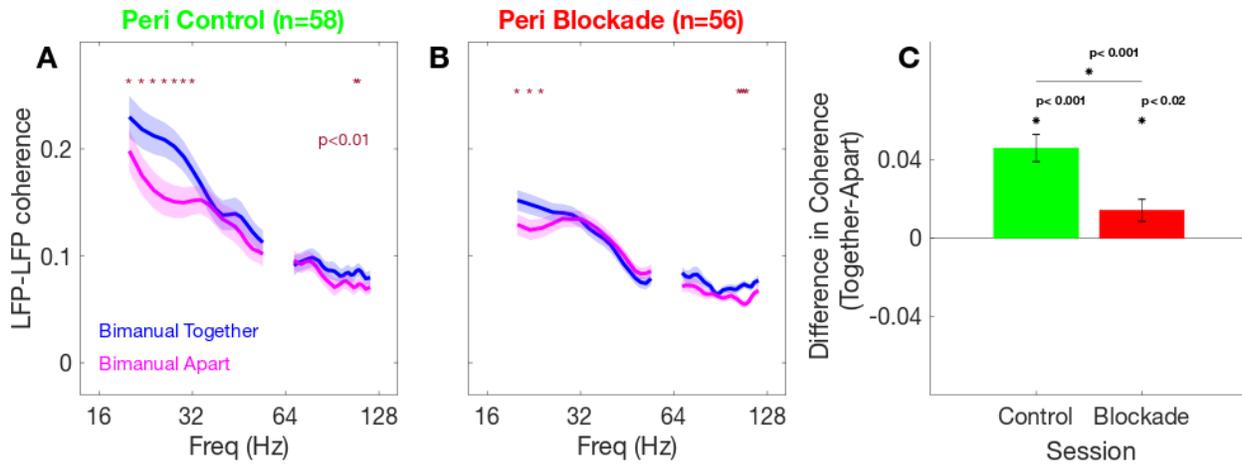
262 Our behavioral results indicate that communication between the left and right PRR helps
263 support bimanual coordination. We looked for neural correlates of this communication
264 by measuring the effect of callosal blockade on interhemispheric LFP-LFP coherence
265 (see Methods) (58). Beta-band LFP activity often correlates with motor control variables
266 (34, 59–65), and interhemispheric LFP-LFP coherence in this band shows bimanual task-
267 specific modulation (22, 35). Interhemispheric coherence is significantly stronger when
268 preparing bimanual-together than bimanual-apart movements and is intermediate when
269 preparing unimanual movements or saccades. This pattern suggests that
270 interhemispheric communication increases when both arms move toward the same
271 target and decreases when each arm moves to a different target. Alternatively, common
272 input may increase for same-target movements and decrease for movements to different
273 targets. If interhemispheric communication is at play, and if it occurs via direct
274 connections between the left and right PRR, then blocking callosal pathways should
275 disrupt or abolish task-specific modulation of LFP coherence, consistent with the effect
276 of blockade on behavior.

277 Interhemispheric coherence is shown in Fig. 4 and Fig. S9. Coherence was tested at 2
278 Hz intervals from 20 to 100 Hz, with a focus on the 20-30 Hz frequency band found to
279 be of particular interest in our previous studies (35, 54). Consistent with previous results,

280 baseline coherence was significantly stronger while planning a bimanual-together
281 movement compared to a bimanual-apart movement at each individual frequency from
282 20 to 32 Hz ($p < 0.01$) as well as in the *a priori* 20-30 Hz band (difference of $0.046 \pm$
283 0.007 , $p < 0.001$; Fig. 4). Callosal blockade reduced this difference by 70% ($p < 0.001$)
284 though it did not completely disappear, particularly at the lowest frequencies tested
285 (0.014 ± 0.006 , $p < 0.02$).

286 We initially hypothesized that callosal communication can explain why, despite single
287 unit activity only distinguishing movements that include the contralateral arm, beta-band
288 LFP modulations are distinct for each of the five movement types that we tested. This
289 hypothesis is supported by the fact that, after callosal blockade, interhemispheric
290 coherence is no longer strongly modulated by whether the two arms move together or
291 apart. However, the beta-band LFP activity continues to show distinct modulations for
292 different patterns of arm movements (Fig. S1C–D).

293 We performed a similar analysis using data from the left and right lateral intraparietal
294 area (LIP) from one animal. The lidocaine injections were targeted based on tract-tracing
295 from PRR, but it is likely that callosal fibers from LIP were also affected. LIP shows no
296 task-specificity in coherence at baseline and no evidence for a change with callosal
297 blockade (Fig. S10).



298 **Fig. 4.** LFP-LFP coherence between left and right PRR in control and callosal blockade
299 sessions.
300 (A) Coherence is higher for bimanual-together movements than for bimanual-apart
301 movements at 20-32 Hz. Red asterisks denote differences of $p < 0.01$, tested at 2 Hz
302 intervals averaged over 58 pairs of electrode contacts in each hemisphere. Shaded
303 regions represent \pm SEM. (B) During the Peri callosal blockade blocks, the bimanual-task
304 specific difference in coherence is reduced at low frequencies and abolished at higher
305 frequencies. Format as in a. (C) Blocking the corpus callosum significantly reduced the
306 task-dependent difference in coherence measured from 20-30 Hz ($p < 0.001$, pooled t-
307 test). This frequency range, 20-30 Hz, was specified prior to the start of data collection
308 to avoid multiple comparison issues. Error bars are \pm SEM.

309 **Discussion**

310 Effective bimanual coordination depends on interhemispheric communication via the
311 corpus callosum. Here, we examined the contributions of callosal connections between
312 left and right PRR in mediating these effects. To identify the specific callosal channels
313 involved, we first mapped interhemispheric projections using manganese-enhanced MRI
314 tract-tracing. This revealed that PRR-PRR callosal projections are restricted to the
315 splenium. We then reversibly blocked these splenial fibers and assessed behavioral and
316 neural consequences. Compared to baseline, callosal blockade reduced the temporal
317 synchrony of bimanual-together movements (Fig. 3A), sped up movement initiation
318 across all tasks (Fig. 3B), and reduced errors in bimanual-apart movements (Fig. 3C),
319 suggesting an inhibitory role for callosal communication (44, 66, 67). Neural recordings
320 were complementary to the behavioral findings: task-specific LFP-LFP coherence
321 between left and right PRR was selectively reduced during bimanual tasks during callosal
322 blockade (Fig. 4). Together, these results suggest that the posterior corpus callosum
323 actively modulates bimanual movement planning.

324 The corpus callosum is the largest white-matter commissure, integrating sensory, motor,
325 and cognitive processes across the cerebral hemispheres. It is topographically
326 organized, with distinct regions supporting specific interhemispheric functions (68–71).
327 Studies of split-brain patients who have undergone callosotomy surgeries provide
328 valuable insights into hemispheric interactions. Studies of these patients implicate the
329 corpus callosum in bimanual coordination (47, 48, 72–74) with deficits emerging in novel
330 or complex tasks while well-learned movements remain intact (48, 75). However, prior
331 studies have either assessed behavior without measuring neural changes, or examined

332 interhemispheric connectivity without linking it to behavior (76–82). This study directly
333 establishes a causal relationship between bimanual coordination and interhemispheric
334 connectivity.

335 Complete commissurotomy limits the ability to determine specific cortical contributions
336 to interhemispheric interactions. Studies of partial or staged commissurotomy have
337 revealed region-specific contribution of the corpus callosum to bimanual coordination.
338 Severing the anterior corpus callosum primarily affects temporal synchronization and
339 movement initiation (45, 46, 83, 84). In contrast, severing the posterior corpus callosum
340 impairs spatial coordination and directional control (45, 47, 85). Such approaches offer
341 only coarse localization and are irreversible, limiting their utility in pinpointing
342 contributions of specific callosal pathways. By focally and reversibly blocking the
343 posterior corpus callosum, we specifically evaluated the role of callosal pathways
344 between the two PRRs in neural communication and behavioral performance.

345 Our results indicate that the posterior corpus callosum facilitates temporal coordination
346 of spatially coordinated bimanual movements. Blocking the splenium disrupted
347 synchrony in bimanual-together movements but did not affect synchrony in bimanual-
348 apart movements, suggesting its role is specific to spatially coordinated actions rather
349 than independent limb control. This aligns with prior studies implicating the posterior
350 corpus callosum in the spatial coordination of bimanual movements (45, 48, 85).

351 Callosal blockade also led to faster movement initiation across all tasks, suggesting that
352 interhemispheric communication, specifically between homotopic areas such as PRR,
353 normally exerts a functionally inhibitory influence on movement onset. Interestingly, error

354 rates decreased selectively during bimanual-apart movements during blockade. This
355 finding is consistent with case studies of posterior callosotomy patients, where
356 asymmetric or independent limb movements sometimes improve (45, 47).

357 Motor behavior appears to begin from a “mirror” program: during movement planning,
358 regions such as dorsal premotor cortex and supplementary motor area exhibit bilateral
359 activation (86–88). To produce lateralized, unimanual actions, the brain engages
360 interhemispheric inhibitory mechanisms, whereby the active motor cortex suppresses its
361 counterpart (ipsilateral to the intended movement), typically via excitatory callosal
362 projections that engage inhibitory interneurons in the opposite hemisphere (89–91).
363 However, the corpus callosum is not the only determinant of motor lateralization.
364 Congenital absence of the corpus callosum can produce a syndrome in which
365 movements on both sides of the body become coupled, suggesting that additional
366 anatomical pathways contribute to the ability to produce lateralized actions (92). These
367 likely include subcortical structures such as the corticospinal tract and the spinal cord
368 (93–95), but their roles remain to be fully defined.

369 While our tasks were not specifically designed to assess bimanual movement symmetry,
370 we were able to classify movement types post hoc based on both symmetry and
371 laterality. Callosal blockade had no significant effect on movement errors or RTs when
372 movements were grouped by symmetry (Fig. S7 and Fig. S8). However, we observed a
373 significant effect of blockade when bimanual movements were grouped by laterality,
374 specifically whether they were crossed (Fig. S7). Because each cerebral hemisphere
375 primarily processes spatial information from the contralateral visual hemifield, crossed
376 movements typically require interhemispheric transfer since the hemisphere that

377 perceives the spatial target must communicate with the opposite hemisphere to initiate
378 the motor response. Thus, one might expect callosal blockade to impair performance of
379 crossed movements. Instead, we found that callosal blockade significantly reduced
380 errors in crossed bimanual movements. This improvement suggests that
381 interhemispheric communication may introduce interference in this condition, and that
382 reducing callosal input may improve performance by allowing each hemisphere to
383 process and respond independently. These findings also imply that other cortical or
384 subcortical pathways may be sufficient to support lateralized action planning.

385 Task-specific LFP-LFP coherence between left and right PRR was reduced or abolished
386 during callosal blockade, indicating a loss of interhemispheric communication (Fig. 4 and
387 Fig. S9). This disruption was specific to bimanual tasks and suggests that
388 interhemispheric coupling of left and right PRR contributes to coordinating bilateral
389 movement plans. The loss of beta-band task-specific coherence corresponds with the
390 decrease in temporal synchrony for bimanual-together movement RT, suggesting that
391 interhemispheric communication plays a role in maintaining coordinated timing between
392 the arms.

393 Mooshagian and colleagues found that PRR unit activity primarily reflects contralateral
394 arm movement plans, whereas local beta-band LFP encodes both contralateral and
395 ipsilateral arm movements (35). A key hypothesis was that ipsilateral arm information in
396 PRR beta-band LFP activity originates from PRR in the opposite hemisphere via callosal
397 projections, an idea supported by the interhemispheric PRR-PRR beta coherence
398 findings. However, splenium blockade did not abolish local beta-band task specificity in

399 PRR (Fig. S1C–D). This suggests that beta-band activity in PRR does not rely exclusively
400 on direct callosal input from the opposite PRR.

401 One explanation is that callosal blockade is incomplete, leaving many alternative
402 interhemispheric communication pathways intact. The splenium itself may not be
403 completely blocked by our method, and other callosal pathways or subcortical
404 connections may still contribute to interhemispheric movement encoding. Mooshagian
405 and colleagues (35) (see their Supplementary Table 3) proposed that beta power
406 differentiation is due to a mixture of local and contralateral input, with even a small
407 amount (5-20%) of contralateral input sufficient to maintain movement type selectivity in
408 beta-band activity. The persistence of PRR beta-band LFP selectivity following splenium
409 blockade is therefore consistent with the idea that a small amount of contralateral arm
410 information – whether via residual splenial fibers, alternative callosal channels, or extra-
411 callosal pathways – is sufficient to maintain beta-band movement encoding. An
412 alternative explanation is that the beta-band LFP task selectivity reflects differences in
413 the visual input. This could explain the difference between tasks with one versus two
414 targets, but not the differences between single target tasks.

415 Theories of callosal function propose that interhemispheric communication can be either
416 excitatory or inhibitory, with human studies providing evidence of both mechanisms (35,
417 53, 96–98). Faster movement initiation across tasks suggests that callosal projections
418 may normally exert an inhibitory influence on movement initiation. Conversely, the
419 disruption of synchrony in bimanual-together movements suggests that PRR-PRR
420 callosal projections facilitate temporal coordination in spatially aligned movements,
421 possibly through excitatory coupling. The fact that bimanual-apart movements were not

422 affected suggests that this coordination is specific to movement requiring spatial and
423 temporal alignment, and is not a general property of bimanual coordination. It is
424 important to keep in mind that the functional effects of interhemispheric communication
425 do not constrain whether the callosal fibers themselves are excitatory or inhibitory (44,
426 50).

427 A limitation of our approach is that callosal blockade likely affects more than just PRR-
428 PRR connections, potentially impacting nearby areas such as LIP (99, 100). A preliminary
429 study using the same methods indicates substantial overlap between callosal pathways
430 from LIP and PRR within the splenium. While our focal blockade altered eye-hand
431 coordination behaviorally, it did not affect neural communication between PRR and LIP
432 or between LIP and LIP in each hemisphere (Fig. S10; J. Kang, E. Mooshagian, L. H.
433 Snyder. Temporal eye-hand coordination may be subserved by connections between
434 PRR and LIP. Neuroscience Meeting Planner. Washington, DC: Society for
435 Neuroscience, 2023. Online.). More precise targeting methods, such as optogenetics or
436 chemogenetics, could clarify the specific role of PRR-PRR callosal pathways in motor
437 coordination (101, 102).

438 Understanding long-range communication between different brain regions is essential
439 for both basic neuroscience and clinical applications (103–106). Our Mn-MRI approach
440 for mapping specific callosal pathways can be extended to investigate interhemispheric
441 working memory transfer, white-matter contributions to visual processing, or other forms
442 of hemispheric integration (107–109). Future studies using varied behavioral paradigms
443 and selective circuit manipulations will be necessary to further elucidate the neural and
444 behavioral contributions of long-range communication.

445 **Materials and Methods**

446 **Experimental model and subject details.**

447 All procedures conformed to the Guide for the Care and Use of Laboratory Animals and
448 were approved by the Washington University Institutional Animal Care and Use
449 Committee. Two male rhesus macaques (*Macaca mulatta*), Monkey J (7-year-old male,
450 14.5 kg) and Monkey T (20-year-old male, 9.0 kg), were used in the study.

451 **Apparatus.**

452 Head-fixed animals sat in a custom-designed monkey chair (Crist Instrument,
453 Hagerstown, MD) with an open front for unimpaired reaching movements with both arms.
454 Visual stimuli were back-projected by an LCD projector onto a translucent plexiglass
455 screen mounted vertically ~40 cm in front of the animal. The room was otherwise dark.
456 Eight target positions were organized in a rectangle centered on the fixation point, each
457 target ~8 cm (11°) or ~11 cm (15°) from the center fixation point. A small piece of
458 plexiglass (5 cm × 1 cm) oriented in the sagittal plane was mounted on the front of the
459 projection screen to bisect the touching surface at each target location. The animals
460 were trained to reach with the left hand to the left side of the divider and the right hand
461 to the right side. Touches were monitored every 2 ms using 16 capacitive sensors,
462 mounted on the back of the screen, one sensor on each side of each of the 8 possible
463 target locations to sense reach endpoints. Thus, each hand activated a unique capacitive
464 sensor, even when both hands reached the same target. Two additional sensors, one
465 sensor at each of the two home pads, were used to monitor the animals' reach starting

466 positions and one sensor on each side of each of the 8 possible target locations to sense
467 reach endpoints. Thus, each hand activated a unique capacitive sensor, even when both
468 hands reached the same target. Eye position was monitored using the 120 Hz ISCAN
469 eye-tracking laboratory (ETL-400). Animals were monitored in the testing room using two
470 infrared cameras equipped with infrared illuminators, aimed at the plexiglass screen and
471 the home pads.

472 **Behavioral tasks.**

473 The task design and the movement conditions are illustrated in Fig. 1. The animals
474 performed delayed saccade-only movements or coordinated eye plus arm movements
475 using the left, right, or both arms. Initially, the animals fixated on a circular white stimulus
476 ($1.5^\circ \times 1.5^\circ$) centered on the screen. Their left and right hands touched “home” pads
477 situated at waist height, 20 cm in front of each shoulder. After maintaining fixation ($\pm 5^\circ$)
478 and initial arm positions for 500 ms, one or two peripheral targets ($5^\circ \times 5^\circ$) appeared on
479 the screen for 1250-1750 ms, during which fixation was required. Next, the fixation target
480 shrank to a single pixel, cueing the animal to move to the peripheral target(s) in
481 accordance with target color and a previously trained code. A green (red) target
482 instructed a reach with the left (right) arm. A red target instructed a reach with the right
483 arm. A blue target instructed a combined reach with both arms (“bimanual-together”).
484 The simultaneous appearance of red and green targets cued a “bimanual-apart” reach,
485 where each arm reached its respective target. For bimanual-apart reaches, the two
486 targets appeared at diametrically opposite locations across the central fixation and the
487 arms could therefore be crossed or uncrossed. A white target instructed a saccade
488 without a reach. To ensure natural coordination, animals were never trained to make arm

489 movements without moving the eyes. All single-target reach trials required an
490 accompanying saccade to the target, while saccades were optional (but almost always
491 performed) for two-target reach trials.

492 All trial types were randomly interleaved within sets of 40 trials (one each per condition
493 [5 task types] and [8 target configurations]). During saccade and unimanual reach trials,
494 the non-moving hand(s) remained on the home button(s). In bimanual together trials, the
495 left and right hands were required to hit their target within 275-325 ms (Monkey J;
496 Bimanual together), 225 ms (Monkey T; Bimanual together), 300-500ms (Monkey J;
497 Bimanual apart), or 300 ms (Monkey T; Bimanual apart). Animals were required to
498 maintain their hand(s) on the final target(s) for 300 ms. The spatial tolerance for saccades
499 was $\pm 5^\circ$. If an error occurred (a failure to achieve or maintain the required eye or hand
500 positions), the trial was aborted, and short time-out ensued (1500ms for early fixation
501 breaks and 500ms for targeting errors). Successful trials were rewarded with a drop of
502 water or juice.

503 **Manganese-enhanced magnetic resonance imaging (Mn-MRI).**

504 Callosal pathways connecting left and right PRR were identified in one animal (Monkey
505 T) with *in vivo* Mn-MRI (56, 57, 110). Two 33-gauge cannulae attached to 10- μ L Hamilton
506 syringes were lowered to two locations in the right PRR. Next, 1.0 μ L of 0.3M $\text{MnCl}_2(\text{H}_2\text{O})_4$
507 in 0.9% sterile saline solution buffered with 10 mM Tris-HCl (pH \sim 7.4) was injected into
508 each site using a microinjection pump (Harvard Apparatus). We acquired MRI images
509 24- and 48-hours after the injection. A subtraction image (48 hr - 24 hr) showed

510 anterograde transport of Mn^{2+} from right PRR. Callosal pathways from right PRR to the
511 left hemisphere were restricted to the splenium (Fig. S2A).

512 **Reversible callosal blockade.**

513 We considered the onset time, duration of inhibitory effects of 2% lidocaine, and the
514 injection volume necessary to observe behavior and neural effects, in designing the Peri
515 block. Pilot experiments established that 5.0 μ L for Monkey J and 5.5 μ L for Monkey T
516 were effective volumes for observing changes in behavior and neural activity. These
517 effects persisted throughout the blockade experiment.

518 The effects from lidocaine injection have faster onset and shorter duration than muscimol
519 (GABA-A receptor agonist) (14, 28, 110, 111). Neural activity is effectively silenced 2
520 minutes after lidocaine injection, and neurons regain their initial activity 30 minutes after
521 lidocaine injection (112, 113). To ensure blockade was in effect, the Peri block
522 commenced only after 1.0 μ L of lidocaine had been injected (6.6 minutes). To maintain
523 blockade at a constant level throughout the block, lidocaine was continuously injected
524 at a constant rate until a total volume of 5.0 μ L (Monkey J) and 5.5 μ L (Monkey T) was
525 reached. Peri blockade blocks were completed within 20 minutes after lidocaine
526 injection.

527 Each blockade session proceeded as follows. A 33-gauge injection cannula attached to
528 a 10- μ L Hamilton syringe was lowered to the splenium. At the same time, recording
529 electrodes were lowered to left and right PRR. The electrodes and cannula were allowed
530 to settle for 15 minutes. Next, animals completed a block of 400 trials (Monkey J) or 480

531 trials (Monkey T) ('Pre', 45 minutes). Next, there was a 40 minute break. Following the
532 break, the Peri block began. The details of the Peri block were informed by the onset
533 time, duration and the injection volume necessary to observe behavior and neural
534 effects. Seven minutes before the Peri block commenced, we began injecting 2%
535 lidocaine at a rate of 0.15 $\mu\text{L}/\text{min}$ using a microinjection pump (Harvard Apparatus). Next,
536 animals completed a second block of 400 trials (Monkey J) or 480 trials (Monkey T)
537 ('Peri', 45 minutes). The Peri block began once 1.0 μL of 2% lidocaine was injected (6.6
538 minutes). A total of 5.0 μL (Monkey J) or 5.5 μL (Monkey T) of lidocaine was injected,
539 ending 27 (Monkey J) or 30 minutes (Monkey T) into the Peri block.

540 Blockade and control sessions differed only by whether lidocaine or a sham injection
541 was performed. For control sessions, either 0.9% saline solution was injected (2 sessions
542 for each Monkey) or nothing (sham) was injected (13 sessions for Monkey J; 7 sessions
543 for Monkey T). In the sham sessions, the procedure was identical to a control session
544 with 0.9% saline solution except that the injection apparatus was set up without an
545 injection cannula.

546 In a subset of sessions, the experimenter was blinded to the session type (blockade or
547 control). For Monkey J, we conducted 1 blinded blockade and 1 blinded control session
548 out of 12 blockade and 15 control sessions, respectively. For Monkey T, we conducted
549 2 blinded blockade and 2 blinded control sessions out of 10 blockade and 9 control
550 sessions, respectively.

551 **Injection localization with MRI.**

552 We administered manganese injections to confirm our focal blockade coordinates. For
553 Monkey J, we injected 0.08 μL of 0.08M $\text{MnCl}_2(\text{H}_2\text{O})_4$ in 0.9% sterile saline solution. For
554 Monkey T, we used 2 μL of 0.06M $\text{MnCl}_2(\text{H}_2\text{O})_4$ in 2% lidocaine solution. Both solutions
555 were buffered with 10 mM Tris-HCl (pH \sim 7.4). We acquired structural MRI images within
556 6 hours after the injection as specified in the section *Mn-MRI*. We observed isolated
557 halos in the splenium in both animals and confirmed the accuracy of our injection sites
558 (Fig. S2B–C).

559 **Electrophysiological recordings.**

560 Simultaneous recordings were made from the left and right hemispheres of Monkeys J
561 and T. Each animal had two recording chambers centered approximately at 8 mm
562 posterior to the ear canals and 12 mm lateral of the midline on each side, placed flush
563 to the skull. Anatomical magnetic resonance images were used to localize the medial
564 bank of the intraparietal sulcus. Extracellular recordings were made using two glass-
565 coated tungsten electrodes (Alpha Omega, Alpharetta, GA; impedance 0.5-3.0 M Ω at
566 1kHz) for both monkeys, or a 32-channel multi-contact electrode (NeuroNexus, Ann
567 Arbor, MI; contacts 200 μm apart; impedance \sim 1.25 M Ω at 1kHz) for Monkey J, inserted
568 through a steel guide tube into PRR in each hemisphere. Neural signals from the four
569 single-contact electrodes or the two multi-contact electrodes were processed and saved
570 using the Plexon MAP system (Plexon, Inc.) for Monkey T and the Open Ephys
571 acquisition system (114) for Monkey J. In the Plexon MAP system, signals were passed
572 through a pre-amplifier and then separated into two signal paths for LFP and spikes. The

573 LFP channel was band-pass filtered between 0.7 and 300 Hz and digitized at 1 kHz. The
574 spike channel was band-pass filtered between 100 Hz and 8 kHz and digitized at 25 kHz.
575 In the Open Ephys system, signals were passed through a pre-amplifier and band-pass
576 filtered between 2.5 and 7603.8 Hz and digitized at 30.0 kHz. Spikes were isolated online
577 via manually-set thresholds for waveform detection triggers. As a measure of
578 interhemispheric communication, we computed LFP-LFP coherence between left and
579 right PRR over a broad range of frequencies. For each session using single-contact
580 electrodes, we computed LFP-LFP coherence for each of the four possible
581 interhemispheric pairings of electrodes. In each session using 32-channel multi-contact
582 electrodes, we used LFP signals from every 4th contact (i.e., we used only 8 of the 32
583 contacts on each electrode, each separated by 800 μm) and we computed 4 average
584 LFP-LFP coherence values from each of the 64 possible interhemispheric pairings of
585 contacts.

586 **Quantification and statistical analysis.**

587 All data analyses were conducted using custom codes written in C, R, and MATLAB.

588 **LFP power.**

589 LFP power spectral density was estimated with a multitaper method. For each trial, the
590 LFP signal was windowed with each of 4 orthogonal Slepian tapers and Fourier
591 transforms were estimated. The Fourier transform of LFP signal $x_n(t)$ with the k^{th} taper,
592 $d_k(t)$ was estimated according to Eq. (1).

593
$$X_{n,k}(f) = \sum_{t=1}^T d_k(t)x_n(t)e^{-2\pi jft} \quad (1)$$

594 $x_n(t)$ is the windowed LFP signal for trial n , T is the length of $x_n(t)$, f is the frequency,
595 and j is the imaginary unit ($\sqrt{-1}$). The power spectral density for a single trial n , $S_{xx,n}(f)$,
596 was then estimated as a weighted average of auto-spectra $|X_{n,k}(f)|^2$ across tapers
597 according to Eq. (2).

598
$$S_{xx,n}(f) = \frac{1}{f_s K} \sum_{k=1}^K w_k |X_{n,k}(f)|^2 \quad (2)$$

599 where f_s is the sampling frequency, K is the number of tapers, and w_k are weights
600 determined by an adaptive algorithm (115). The power spectral density was then
601 averaged across trials to produce a single estimate of the power spectral density
602 according to Eq. (3) where N is the number of trials.

603
$$S_{xx}(f) = \frac{1}{N} \sum_{n=1}^N S_{xx,n}(f) \quad (3)$$

604 We used a time-half-bandwidth product of 2.5, affording us 4 Slepian tapers. We used
605 either 400 ms or 200 ms windows, affording us frequency resolutions of ± 6.25 or ± 12.5
606 Hz, respectively. Band-limited power was estimated by summing the power spectral
607 density estimate over the band of interest. Power time signals were estimated by
608 stepping the time window by either 100 ms (400 ms windows) or 50 ms (200 ms
609 windows) and estimating band-limited power at each time step. We present power time
610 signals and power spectral density as percentage of baseline power or power spectral
611 density, respectively. Baseline values are estimated as the average value over the 500
612 ms before target presentation. Power was computed at each LFP recording site
613 individually before averaging across the population.

614 The bands of interest 20-30 Hz were not selected a priori. Instead, these bands were
615 selected empirically early in our study to capture general trends in the power density
616 spectra and then maintained as we collected more data. Note that with a frequency
617 resolution of ± 6.25 Hz (400 ms time windows), the band labeled 20-30 Hz includes
618 information from frequencies from 14 Hz to 36 Hz. The same is true for measures of
619 coherence described below.

620 **LFP-LFP coherence.**

621 We computed LFP-LFP coherence over a broad range of frequencies between left and
622 right PRR during the last 500 ms of a variable delay period prior to the cue to initiate the
623 reach.

624 Shared information between two LFP signals was quantified using coherence. Power
625 spectral densities were estimated with the same multitaper method described above.
626 Coherence between two LFP signals, x and y , was estimated according to Eq. (4).

$$627 \quad C_{xy}(f) = \frac{S_{xy}(f)}{\sqrt{S_{xx}(f)S_{yy}(f)}} \quad (4)$$

628 where $S_{xx}(f)$ and $S_{yy}(f)$ are the mean power density spectra across trials for LFP signals
629 x and y , respectively, and $S_{xy}(f)$ is the cross spectrum for LFP signals x and y , averaged
630 across all trials. The cross-spectrum for a single trial n , $S_{xy,n}(f)$ was estimated as a
631 weighted average of the cross-spectra across tapers according to Eq. (5).

$$632 \quad S_{xy,n}(f) = \frac{1}{f_s K} \sum_1^K w_k X_{n,k}(f) Y_{n,k}^*(f) \quad (5)$$

633 where $X_{n,k}(f)$ and $Y_{n,k}(f)$ are the Fourier transforms of time series $x(t)$ and $y(t)$,
634 respectively, and $Y_{n,k}^*(f)$ is the complex conjugate of $Y_{n,k}(f)$. The mean cross spectrum
635 across trials is then estimated according to Eq. (6) where N is the number of trials.

$$636 \quad S_{xy}(f) = \frac{1}{N} \sum_{n=1}^N S_{xy,n}(f) \quad (6)$$

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641 **Data and Materials Sharing.**

642 Original data created for the study are or will be available in a persistent repository upon
643 publication.

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911 **Supplemental Information for**

912 **A causal role for the posterior corpus callosum in bimanual**
913 **coordination**

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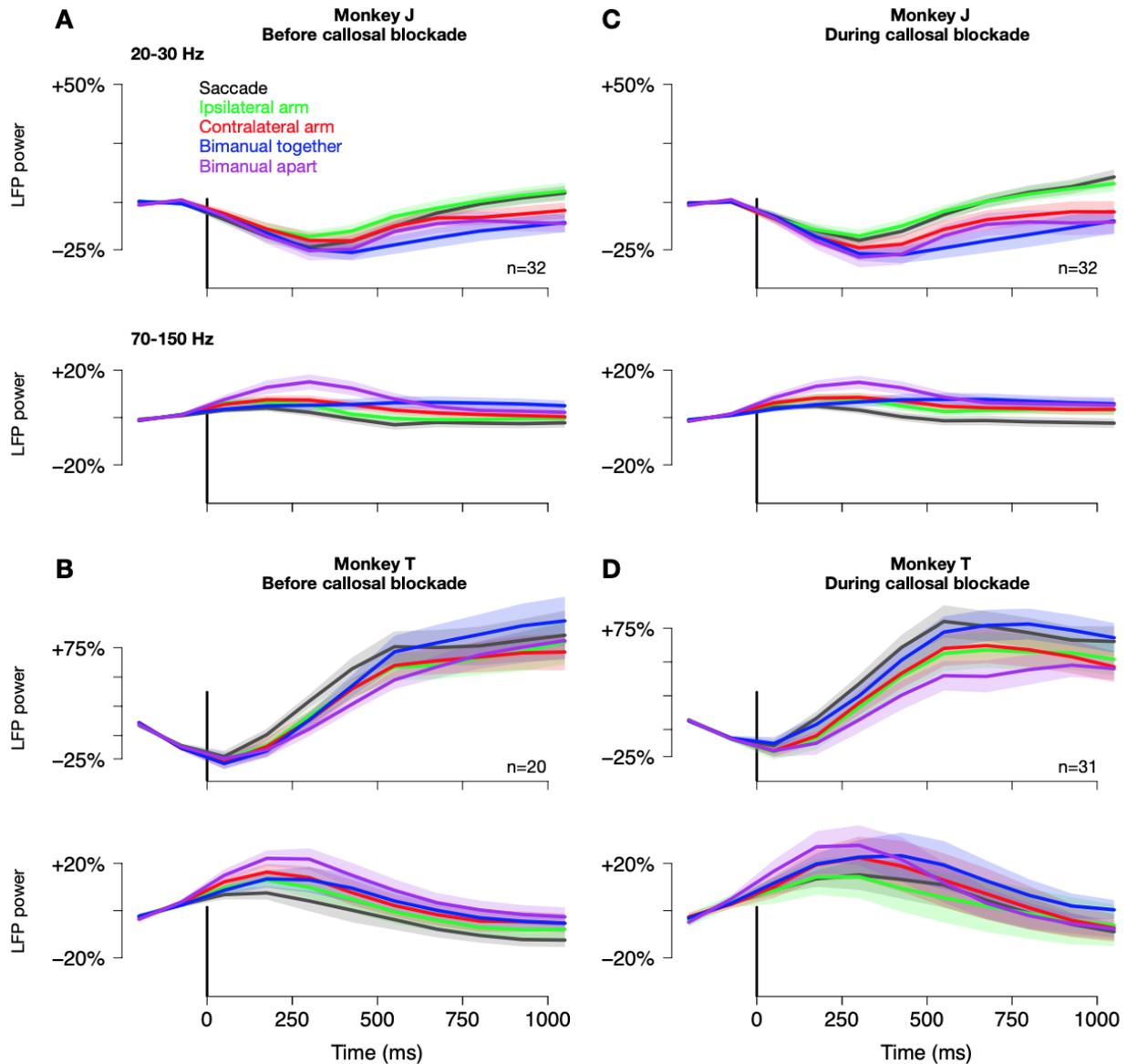
920 *Corresponding author: kang@eye-hand.wustl.edu

921 **This PDF file includes:**

922 Figures S1 to S10

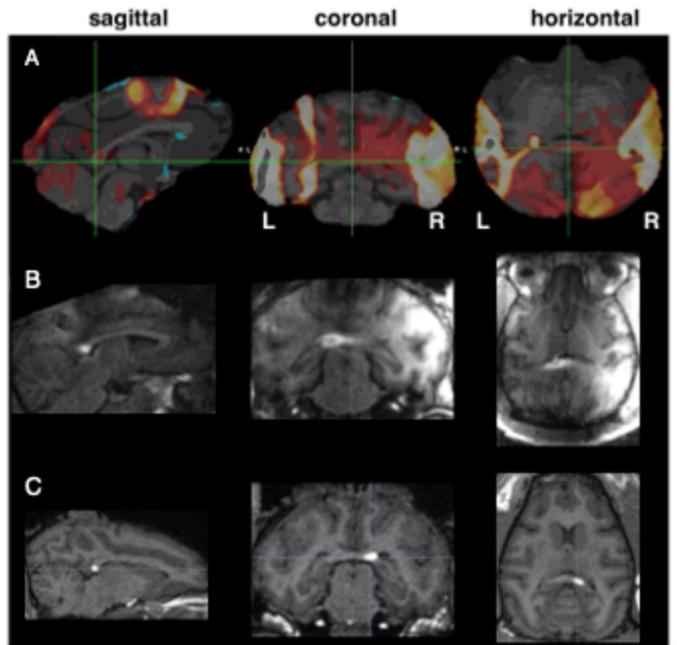
923 Table S1

924 SI Reference

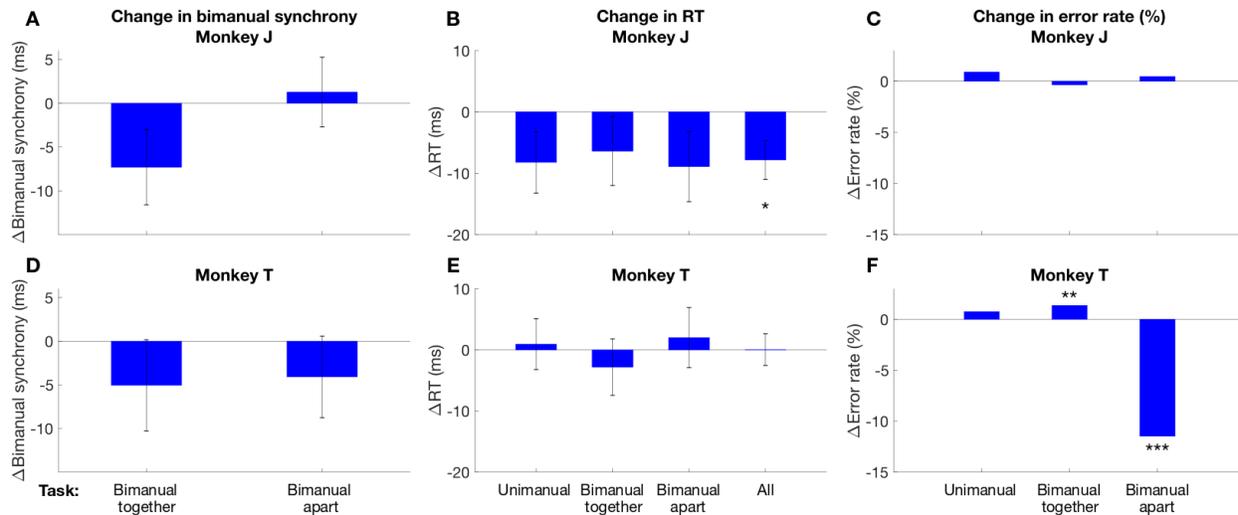


925 **Fig. S1.** PRR LFP power aligned to target onset across the five movement tasks.

926 (A) LFP power in 20-30 Hz (beta-band) and 70-150 Hz (gamma-band) in Monkey J before callosal blockade. (B) LFP
927 power in 20-30 Hz and 70-150 Hz in Monkey J during callosal blockade. (C) LFP power in 20-30 Hz and 70-150 Hz in
928 Monkey T before callosal blockade. (D) LFP power in 20-30 Hz and 70-150 Hz in Monkey T during callosal blockade.
929 Shaded regions in all panels denote \pm SEM. n denotes the number of sites for LFP recordings, which is much smaller
930 than in the previous study where task-specific LFP power modulation ($n = 312$) was demonstrated (Mooshagian et al.,
931 2021).

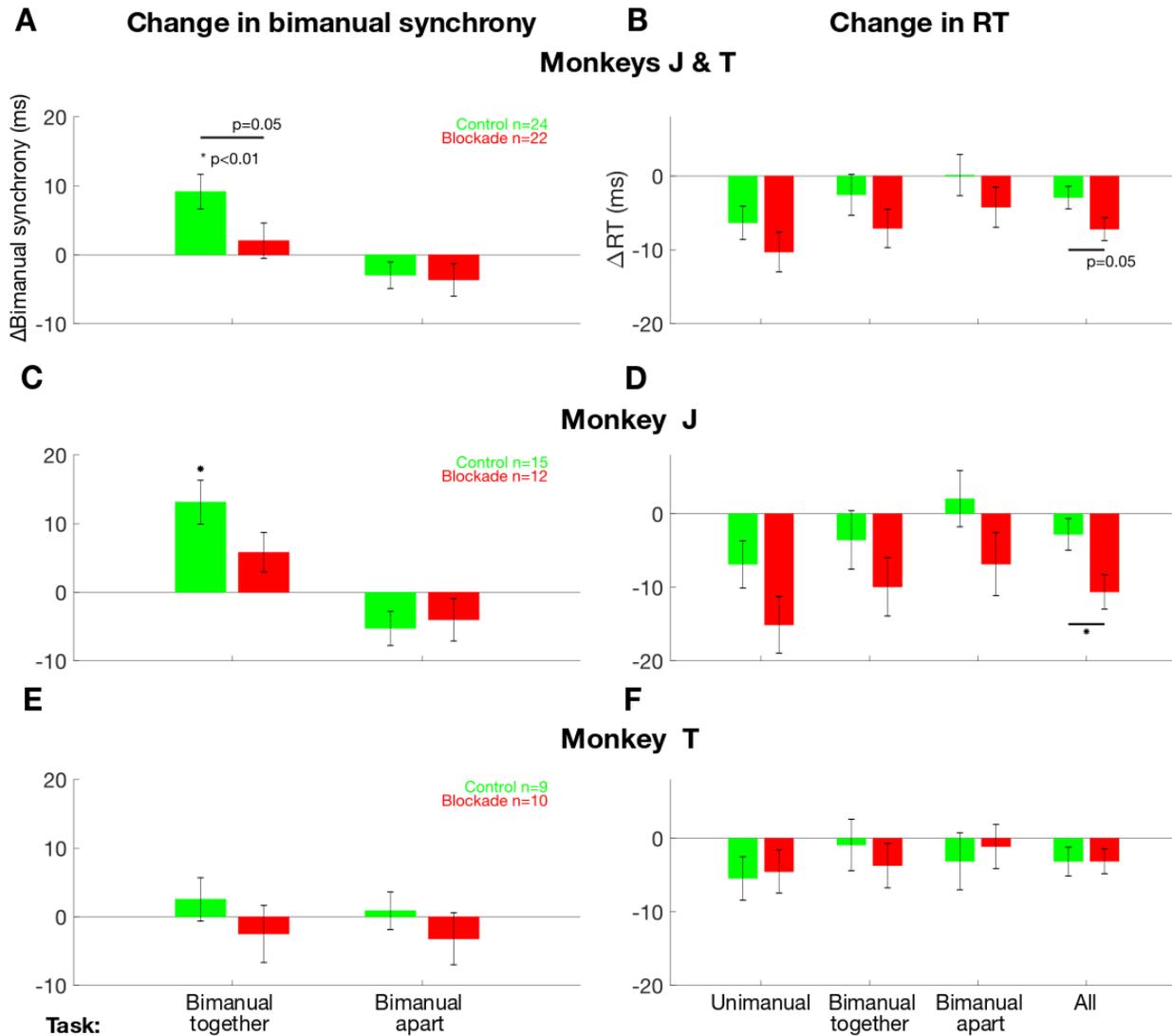


932 **Fig. S2.** In vivo mapping of corpus callosum pathways using manganese-enhanced MRI.
933 (A) Visualization of anterograde transport of manganese from right PRR in Monkey T. 1 μ L of 0.1M MnCl_2 buffered
934 with 10 mM Tris-HCl was injected into right PRR. Structural MR images were acquired 24- and 48-hours post-
935 injection. This is a subtraction MR image: 48 hr - 24 hr after the injection. The green crosshair indicates the callosal
936 pathways from right PRR crossing to the left hemisphere. Callosal pathways connecting left and right PRR were
937 restricted to the splenium. (B) Targeting of injections into the posterior callosum (Monkey T). Images are from awake
938 scans acquired with a custom-made 8-channel coil. The image was acquired 6 hours after injecting 1 μ L of 0.1M
939 MnCl_2 buffered with 10 mM Tris-HCl into the splenium. (C) Targeting of injections into the posterior callosum (Monkey
940 J). Images are from an anesthetized scan acquired with 15-channel knee coil while the animal was anesthetized with
941 isoflurane. The image was acquired 3 hours after injecting 0.08 μ L of 0.1M MnCl_2 buffered with 10 mM Tris-HCl into
942 the splenium. We injected 2% lidocaine solution using the left recording chamber in Monkey T and the right chamber
943 in Monkey J. We did not observe a lateralized effect; there was no behavioral effect specific to the contralateral arm
944 to the side of the chamber used for 2% lidocaine injections.



945 **Fig. S3.** Behavioral performance in callosal blockade and control sessions in each animal.

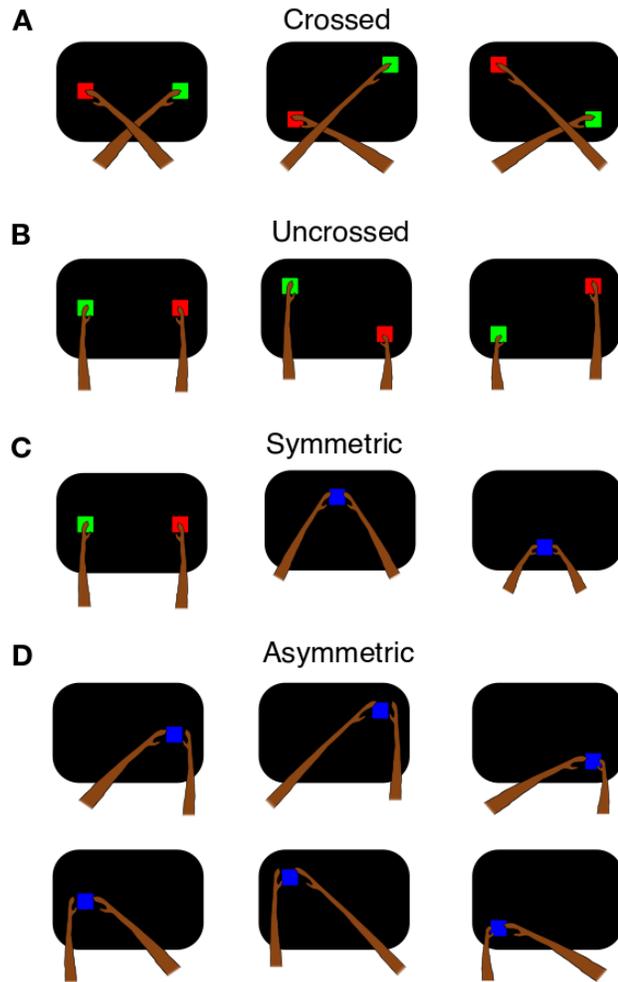
946 Format same as Fig. 3. (A-C) Monkey J. (D-F) Monkey T. (A) There was a trend in callosal blockade de-synchronizing
 947 bimanual-together movements in Monkey T by 7 ms ($p = 0.1$, pooled t-test). (B) Callosal blockade resulted in faster
 948 RT across all uni- and bimanual movements ($p < 0.05$, pooled t-test). (C) No significant change in error rate in Monkey
 949 J. (D) No significant change in bimanual synchrony in Monkey T. (E) No significant change in RT in Monkey T. (F)
 950 Callosal blockade worsened bimanual-together movements ($p < 0.01$, logistic regression) and improved bimanual-
 951 apart movements ($p < 0.001$, logistic regression) in Monkey T. Error bars indicate \pm SEM. * $p < 0.05$; ** $p < 0.01$; *** p
 952 < 0.001



953 **Fig. S4.** Bimanual synchrony and RT shown separately for control and blockade sessions.

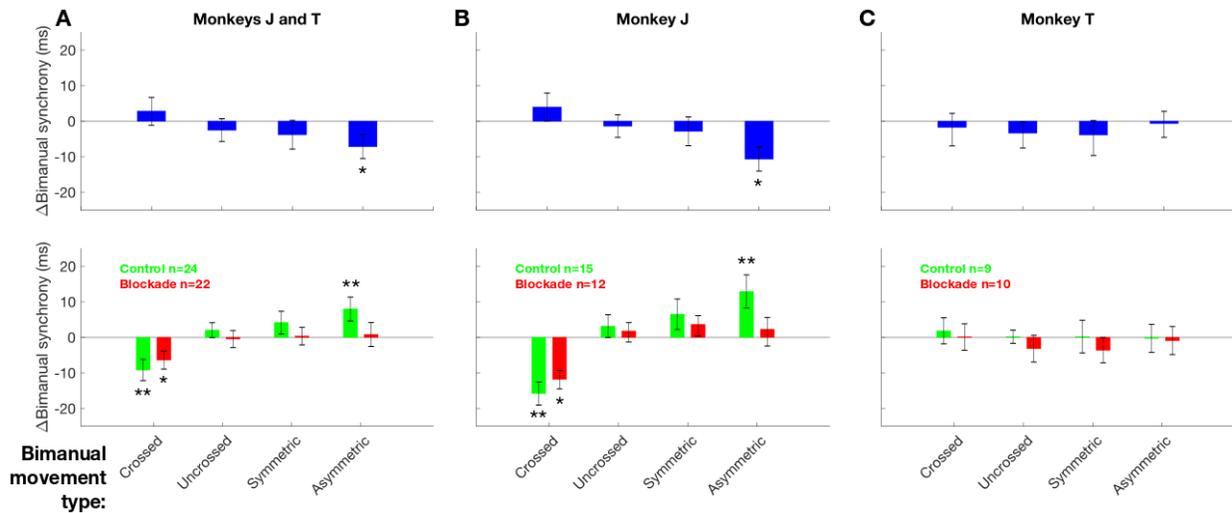
954 (A) Bimanual synchrony as a function of bimanual movement type and session in Monkeys J and T. We assayed the
 955 effect of callosal blockade on the absolute reaction time difference between the two arms, $\Delta(|RT_{Left} - RT_{Right}|)$, in Peri
 956 minus Pre blocks. In control sessions, bimanual-together movements showed increased synchrony (decreased
 957 absolute timing difference) across blocks. This increase was significantly reduced in callosal blockade sessions ($p =$
 958 0.05 , two-sample t-test). No significant changes were observed in bimanual-apart trials. (B) Change in RT between
 959 blocks as a function of movement type and session in Monkeys J and T. Callosal blockade sped movement initiation
 960 (shorter RTs) compared to control for all three movement types. This speeding effect was statistically significant when
 961 averaged across all movement types ($p = 0.05$, two-sample t-test). $\Delta RT(Peri - Pre)$ is calculated as the difference
 962 between the median RT in the Peri block and the median RT in the Pre block for each movement type in both control
 963 and callosal blockade sessions. (C) Blockade desynchronized the two arms for bimanual together movements in

964 Monkey J. In control sessions, the synchrony of bimanual together movements increased (the absolute timing
965 difference decreased) in Peri compared to Pre blocks by -13 ms (paired t-test, $p = 0.001$). In callosal blockade
966 sessions, there was no significant improvement in temporal synchrony of bimanual together movements, indicating a
967 role of the callosum in bimanual movements to a single target. There was no effect on bimanual apart trials. (D)
968 Blockade sped reach initiation in Monkey J. Blockade sped movements (shortens RTs) in all 3 cases compared to
969 control, with a significant effect for All movement types ($p < 0.02$, two-sample t-test). (E) No significant difference in
970 change in bimanual synchrony between control and callosal blockade sessions in Monkey T. (F) No significant
971 difference in change in RT between control and callosal blockade sessions in Monkey T. Error bars in all panels denote
972 \pm SEM.

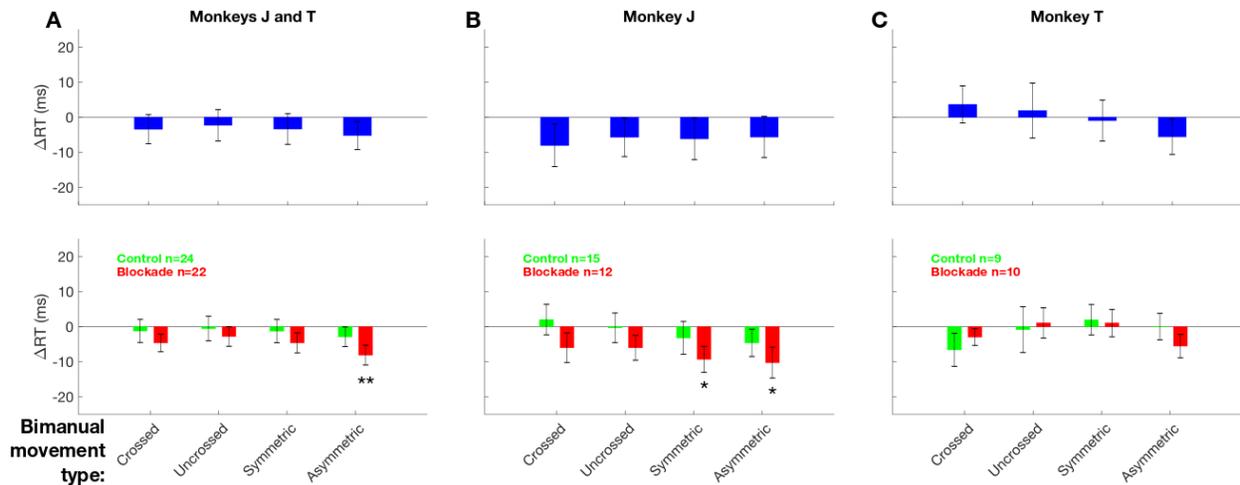


973 **Fig. S5.** Bimanual movement types grouped by laterality (crossed or uncrossed) and symmetry (symmetric or
974 asymmetric).

975 (A) Crossed movements are bimanual-apart movements in which each arm reaches to a target in the contralateral
976 visual hemifield (i.e., left hand to right visual field; right hand to left visual field). These movements require
977 interhemispheric transfer because the hemisphere processing the spatial location of the target differs from the one
978 generating the motor output. (B) Uncrossed movements are bimanual-apart movements in which each arm reaches
979 to a target in the ipsilateral visual hemifield (i.e., left hand to left visual field; right hand to right visual field). Each
980 hemisphere can process the spatial location of the target and generate the motor command locally, without requiring
981 interhemispheric integration. (C) Symmetric movements are bimanual movements in which both arms move to spatially
982 mirror-symmetric locations across the vertical midline. (D) Asymmetric movements are bimanual-together
983 movements in which both arms move to the same lateralized target (e.g., both hands reach to a target in the left visual field),
984 resulting in spatially asymmetric arm movements.



985 **Fig. S6.** Mean change in movement synchrony across bimanual movement types grouped by laterality and symmetry.
 986 We quantified change in bimanual synchrony across different types of bimanual movements based on laterality and
 987 symmetry. Error bars in all panels denote \pm SEM.
 988 Upper row: Format same as in Fig. 3A. We compared the change in bimanual synchrony from Pre to Peri blocks in
 989 control and blockade sessions. Statistics are based on two sample t-tests ($* p < 0.05$)
 990 Lower row: The change in bimanual synchrony from Pre to Peri blocks in control (green) and blockade (red) sessions
 991 shown separately. Statistics are based on paired t-tests ($* p < 0.05$; $** p < 0.01$).
 992 (A) In Monkeys J and T, bimanual synchrony for asymmetric bimanual movements was significantly worse in blockade
 993 sessions compared to control sessions (blue bar; -7.2 ± 3.4 ms; $p < 0.05$). Crossed movements were less synchronous
 994 in Peri blocks in both control ($p < 0.01$) and blockade ($p < 0.05$) sessions. Asymmetric movements were more
 995 synchronous in Peri blocks in control sessions ($p < 0.01$). (B) In Monkey J, bimanual synchrony for asymmetric
 996 bimanual movements was significantly worse in blockade sessions compared to control sessions (blue bar; -10.7 ± 4.7
 997 ms; $p < 0.05$). Crossed movements were less synchronous in Peri blocks in both control ($p < 0.01$) and blockade ($p <$
 998 0.05) sessions. Asymmetric movements were more synchronous in Peri blocks in control sessions ($p < 0.01$). (C) No
 999 significant effect in bimanual synchrony in Monkey T.

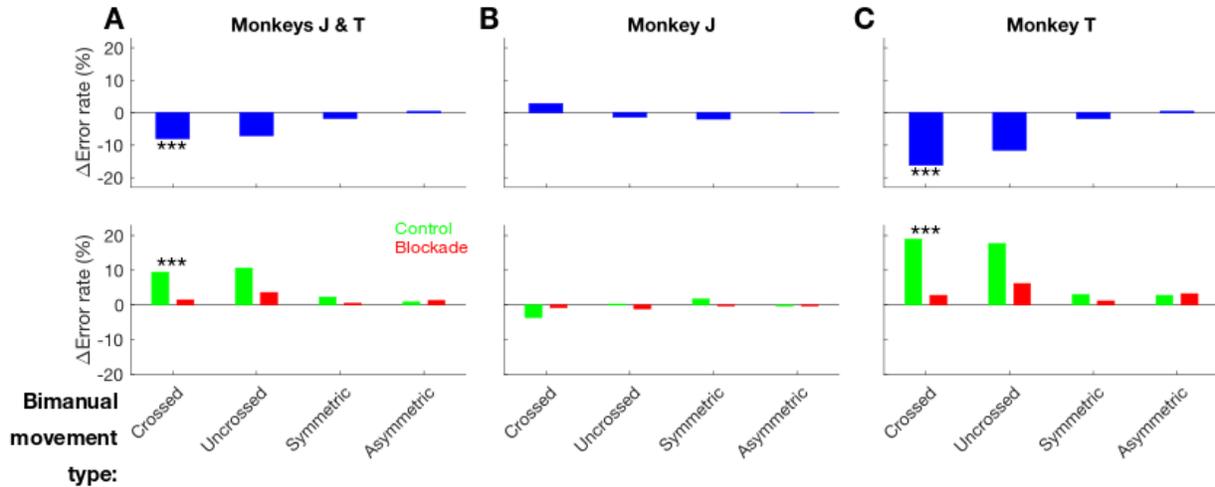


1000 **Fig. S7.** Change in RT in bimanual movement types grouped by laterality and symmetry.

1001 We quantified change in RT across different types of bimanual movements as grouped in Fig. S6. Error bars in all
1002 panels denote \pm SEM.

1003 Upper row: Format same as in Fig. 3B. We compared the change in RT from Pre to Peri blocks in control and blockade
1004 sessions. Lower row: The change in RT from Pre to Peri blocks in control (green) and blockade (red) sessions shown
1005 separately. Statistics are based on paired t-tests (** $p < 0.01$; * $p < 0.05$).

1006 (A) In Monkeys J and T, there was no significant change in RT when comparing blockade vs. control sessions (blue
1007 bars) or in blockade (red) and control (green) sessions separately except for asymmetric movements in blockade
1008 sessions ($p < 0.01$). (B) In Monkey J, there was no significant change in RT when comparing blockade and control
1009 sessions (blue bars). However, symmetric and asymmetric movements had faster RT in Peri blocks in blockade
1010 sessions ($p < 0.05$). (C) No significant effect in RT in Monkey T.



1011 **Fig. S8.** Change in arm error rates in bimanual movement types grouped by laterality and symmetry.

1012 We quantified change in error rates across different types of bimanual movements as grouped in Fig. S6. Δ Error rate

1013 (Peri - Pre) is calculated as the difference between error rates in the Peri block and Pre block.

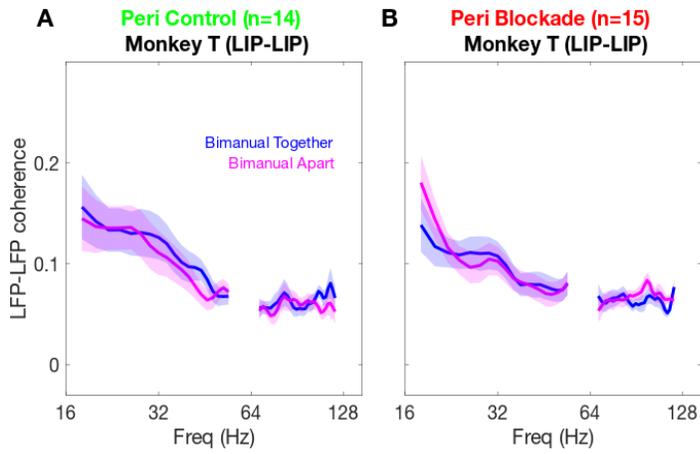
1014 Upper row: We compared the change in error rates in control and blockade sessions.

1015 Lower row: Δ Error rate (Peri - Pre) shown separately for control and blockade sessions.

1016 (A) Crossed arm movements significantly improved by 8% ($p < 0.001$, logistic regression) in callosal blockade sessions

1017 in Monkeys J and T. (B) No clear effect on error rate in Monkey J. (C) Crossed arm movements significantly improved

1018 by 16% ($p < 0.001$, logistic regression) in callosal blockade sessions in Monkey T.



1030 **Fig. S10.** LFP-LFP coherence between left and right LIP in a delayed memory task (Monkey T).

1031 Format same as in Fig. 4A–B. There was no significant task-specific modulation in LFP-LFP coherence in 20-30 Hz

1032 between left and right LIP in (A) Peri Control (0.014 ± 0.012) and (B) Peri Blockade (0.003 ± 0.009) in Monkey T.

Error type	Session			
	Control ($n = 24$)		Blockade ($n = 22$)	
Movement type	Pre	Peri	Pre	Peri
A Eye movement, before Go Cue:				
Saccade-only	14	17	15	16
Unimanual	15	14	12	11
Bimanual-together	16	15	13	15
Bimanual-apart	11	12	11	11
B Eye movement, after Go Cue:				
Saccade-only	2	2	2	3
Unimanual	1	1	1	1
Bimanual-together	1	1	1	0
Bimanual-apart	0	0	0	0
C Arm movement, before Go Cue:				
Saccade-only	0	1	0	0
Unimanual	0	1	1	1
Bimanual-together	0	1	1	1
Bimanual-apart	0	1	1	0
D Arm movements, after Go Cue:				
Saccade-only	1	1	0	0
Unimanual	3	3	2	3
Bimanual-together	4	4	3	5
Bimanual-apart	4	8	3	5

1033 Values are shown as the mean percentage.

1034 **Table S1.** Mean eye and arm error rates (%).

1035 (A) Most eye errors occurred before the Go Cue and were due to premature saccade initiation. (B) Eye errors after the
 1036 Go Cue were due to inaccurate saccade endpoints. (C) Arm errors before the Go Cue were due to premature arm
 1037 movement initiation. (D) Arm movement errors after the Go Cue were due to inaccurate reach endpoints. Most arm
 1038 errors occurred after Go Cue. Error rates are lower than those shown in Fig. 3 because the error rates in this table are
 1039 averaged over sessions while the error rates in Fig. 3 are calculated by merging all success and error trials into a single
 1040 session for binomial test. Because of the scarcity of arm movement errors, we used the binomial test in the main
 1041 analyses.

1042 **SI Reference**

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