

Lateral prefrontal cortex controls interplay between working memory and actions

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1 **ABSTRACT:** Humans must often keep multiple task goals in mind, at different levels of
2 priority and immediacy, while also interacting with the environment. We might need to
3 remember information for an upcoming task while engaged in more immediate actions.
4 Consequently, actively maintained working memory (WM) content may bleed into
5 ongoing but unrelated motor behavior. Here, we experimentally test the impact of WM
6 maintenance on action execution, and we transcranially stimulate lateral prefrontal
7 cortex (PFC) to parse its functional contributions to WM-motor interactions. We first
8 created a task scenario wherein human participants (both sexes) executed cued hand
9 movements during WM maintenance. We manipulated the compatibility between WM
10 and movement goals at the trial level and the statistical likelihood that the two would be
11 compatible at the block level. We found that remembering directional words (e.g., ‘left’,
12 ‘down’) biased the trajectory and speed of hand movements that occurred during the
13 WM delay, but the bias was dampened in blocks when WM content predictably conflicted
14 with movement goals. Then we targeted left lateral PFC with two different transcranial
15 magnetic stimulation (TMS) protocols before participants completed the task. We found
16 that an intermittent theta-burst protocol, which is thought to be excitatory, dampened
17 sensitivity to block-level control demands (i.e., proactive control), while a continuous
18 theta-burst protocol, which is thought to be inhibitory, dampened adaptation to trial-by-
19 trial conflict (i.e., reactive control). Therefore, lateral PFC is involved in controlling the
20 interplay between WM content and manual action, but different PFC mechanisms may
21 support different time-scales of adaptive control.

22

23 **Significance Statement:** Working memory (WM) allows us to keep information active
24 in mind to achieve our moment-to-moment goals. However, WM maintenance may
25 sometimes unintentionally shape our externally-gearred actions. This study formalizes
26 the everyday “action slips” humans commit when we type out or say the wrong word in
27 conversation because it was held in mind for a different goal. The results show that
28 internally maintained content can influence ongoing hand movements, but this interplay
29 between WM and motor behavior depends on the cortical excitability state of the lateral
30 PFC. Neural perturbation with transcranial magnetic stimulation (TMS) shows that
31 temporarily increasing or decreasing PFC excitability can make participants more or less
32 susceptible to the impact of WM on actions.

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36 Actions sometimes come out differently than planned. If motor intentions are at
37 odds with ongoing thoughts, behavior can be skewed. For instance, we might
38 accidentally type out or speak the wrong word aloud if it is going through our mind.
39 Similar ‘action slips’ are exacerbated in patients with frontal cortex damage, who tend to
40 execute behaviors that are inappropriate for the context (Schwartz, 1995). In typical
41 function, such slips may stem from the adaptive role of working memory (WM) in
42 guiding goal-directed behavior. A tight linkage between WM maintenance and motor
43 execution would keep action plans aligned with top-down goals, but might sometimes
44 allow WM content to “leak” into ongoing behavior. Here, we experimentally formalize
45 everyday action slips, and we examine the neural circuitry that modulates the interplay
46 between WM and motor behavior.

47 Although WM is often construed as retrospective storage for past information, its
48 core function may be to guide upcoming behavior (Fuster, 2001; Jin et al., 2020; Olivers
49 & Roelfsema, 2020; Postle, 2006; Theeuwes et al., 2009; van Ede et al., 2019). WM
50 activation might signal that the maintained information is pertinent to current goals,
51 explaining why WM content often captures or biases visual attention (Soto et al., 2005,
52 2008; Soto & Humphreys, 2007). In a prior behavioral study, we found that WM content
53 can also bias hand movements (Miller et al., 2020). During the WM maintenance period
54 for directional word stimuli (e.g., remember ‘left’, ‘down’), cued movements were
55 skewed in a WM-matching direction. Movements were therefore improved if they
56 coincided with WM content but impaired if they conflicted, suggesting that WM may be
57 akin to action preparation (Olivers & Roelfsema, 2020). However, this movement effect
58 was also dampened in task blocks when WM information was less likely to align with
59 movement goals. The interplay between WM content and ongoing motor behavior is
60 therefore adjustable to changing goal states, suggesting that occasional action slips
61 emerge from a generally adaptive system (Carlisle & Woodman, 2011; Kiyonaga et al.,
62 2012; Olivers et al., 2011). This convergence and control between WM and motor
63 behavior could stem from many stages of processing, however, and its source remains
64 to be identified.

65 Lateral prefrontal cortex (PFC) plays a key role in cortico-striatal circuitry for
66 selecting and using WM content to guide behavior (Chatham et al., 2014). The region is
67 thought to monitor and resolve stimulus-response conflict in tasks like the Stroop or
68 Flanker (Botvinick et al., 2001), and WM content may induce similar conflict (Kiyonaga
69 & Egnér, 2014; Pan et al., 2019; Wang et al., 2021). The mid-lateral PFC is also more
70 broadly considered a nexus of cognitive coordination and control (Badre & Nee, 2018;
71 Nee & D’Esposito, 2016). Lateral PFC is a likely candidate to control the interplay
72 between WM and actions, but PFC is multidimensional — it is engaged by a variety of
73 different task demands, shows diverse connectivity, and PFC neurons can exhibit
74 selectivity for various features (Duncan, 2010; Rigotti et al., 2013; Wang et al., 2023).

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75 Likewise, there are competing ideas about the role that human PFC plays in WM and
76 attentional control processes (Curtis & D'Esposito, 2003; Leavitt et al., 2017), and PFC
77 regions may implement distinct forms of control through different circuit mechanisms
78 (Braver, 2012).

79 Here, we ask how lateral PFC contributes to the interplay between WM and
80 concurrent motor behavior. In a dual-task scenario, subjects executed cued hand
81 movements during WM maintenance, and we manipulated the compatibility between
82 WM and action goals from trial-to-trial, as well as the proportion of compatible trials
83 across task blocks. We replicated prior behavioral findings in a baseline condition, and
84 we stimulated left lateral PFC with two transcranial magnetic stimulation (TMS)
85 protocols in experimental comparison conditions. We compared the effects of
86 continuous vs. intermittent theta-burst stimulation (cTBS vs. iTBS), which are thought to
87 have distinct effects on cortical excitability (Huang et al., 2005), subcortical dopamine
88 release (Aceves-Serrano et al., 2022), and network propagation (Cocchi et al., 2015).
89 Whereas cTBS is associated with cortical inhibition, iTBS is associated with excitation.
90 These distinct protocols, delivered to the same region, should therefore serve as strong
91 active controls for one another, to differentiate between functions that rely on the
92 stimulated region. For instance, selective TMS effects on WM performance would
93 implicate the target region in WM storage, while modulation of WM-action compatibility
94 effects would illuminate its role in adaptive control. Moreover, different TMS effects on
95 block-level vs. trial-level indices would illustrate the PFC contribution to superordinate
96 (proactive) task control vs. adapting to immediate changes in (reactive) cognitive control
97 demand. This work will inform the underlying functions that promote WM-driven action
98 slips, clarify the role of PFC in this everyday behavior, and illuminate the cognitive and
99 neural conditions under which these flukes are most likely to occur.

100

101 **Materials and Methods**

102 ***Overview of experimental procedures***

103 On Day 1, participants underwent an anatomical MRI followed by 10 minutes of a
104 resting-state functional MRI. The anatomical MRI was used to stereotactically navigate
105 the TMS coil over the left lateral PFC target. We targeted a PFC region considered part
106 of a cortico-striatal pathway for the selection and use of WM (Chatham et al., 2014;
107 Strafella et al., 2001). After scanning, participants underwent TMS motor thresholding to
108 calibrate the stimulation intensity for TBS sessions. On Days 2-4, participants received
109 either cTBS, iTBS, or a no-TMS baseline condition, and then they completed the
110 behavioral task (**Fig. 1a**). The order of stimulation conditions was counter-balanced
111 across participants.

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112 As in our previous behavioral study (Miller et al., 2020), we used a verbal delayed
113 recognition task, interleaved with a simple motor task during the delay period (**Fig. 1b**).
114 On each trial, participants were instructed to remember a directional WM sample word
115 ('up,' 'down,' 'left,' or 'right'). They were then visually cued to click a screen location (to
116 the top, bottom, left, or right of center). After the cued mouse click, participants were
117 tested on their memory for the sample word. On each trial, we manipulated whether the
118 meaning of the verbal WM content was either compatible (e.g., remember 'left', click
119 inside leftward box) or incompatible (e.g., remember 'left', click inside rightward box)
120 with the direction of the mouse movement action. The performance difference between
121 compatible and incompatible trials (the 'compatibility effect') served as our index of the
122 interplay between WM content and motor behavior. We also varied the proportion of
123 compatible to incompatible trials across blocks of the experiment, so that we could
124 examine the extent to which the compatibility effect is under cognitive control. We then
125 tested how TMS to lateral PFC impacted this control over WM-action interplay.

126

127 **Participants**

128 We aimed for a sample of 24 subjects, with three task sessions each, based on a
129 priori sample size estimation. Power analyses were conducted in G*Power 3.1.9.2
130 (<http://www.gpower.hhu.de>) for repeated-measures ANOVAs, and we considered a
131 range of relevant previous studies to estimate our expected effect size. We considered
132 a previous study from our group that assessed WM after theta-burst TMS to PFC (Lee &
133 D'Esposito, 2012). This study yielded TMS effect sizes in the range of $f(U) = 0.51$ to
134 0.78 , which corresponds to a medium effect. Studies from other groups that applied
135 theta-burst TMS to frontal or parietal cortex in similar within-subject designs report
136 comparable effect sizes within this range, for both TMS main effects and interactions
137 with task conditions (Heinen et al., 2017; Morgan et al., 2013). We used the mean effect
138 size across these studies ($f(U) = .62$) in power calculations, with the power parameter
139 set to $.8$, which yielded a total sample size of 24.

140 We enrolled subjects until we reached this target sample size after exclusions and
141 quality control. Twenty-six subjects (9 male), aged 19-25 (mean: 21.3), were recruited
142 from the Berkeley community, completed informed consent in accordance with the UC
143 Berkeley Institutional Review Board, and were paid \$20 per hour for their participation,
144 plus a \$20 completion bonus for finishing all sessions. Subjects were screened for MRI
145 and TMS contraindications, and reported no history of neurological, psychiatric, or a
146 significant medical condition. Two subjects were excluded from further sessions — one
147 because orthodontic braces produced severe signal distortion in the MRI, and the other
148 revealed a TMS contraindication after initial scanning. Therefore, 24 subjects remain in
149 the reported analyses.

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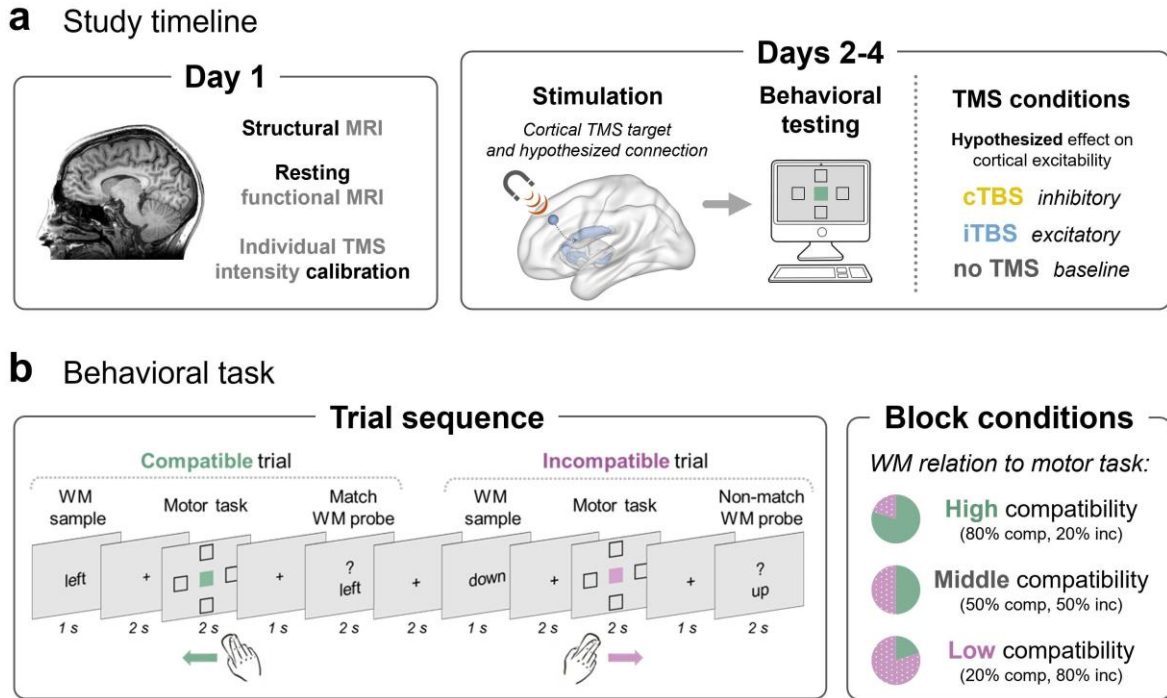


Figure 1. Overview of experimental procedures. (a) On Day 1, participants underwent anatomical and resting-state functional MRI for TMS neuronavigation, then TMS motor thresholding to calibrate their experimental stimulation intensity. On Days 2-4, participants received either a no-TMS baseline condition or one of two experimental TMS protocols to the lateral PFC target, followed by the behavioral task. TMS conditions were given in counterbalanced order on different days. (b) On each trial, participants were first shown a WM sample word to remember ('up,' 'down,' 'left,' or 'right'), then were cued to click one of four screen locations. They were then given a same/different recognition memory test for the sample word. The meaning of the verbal WM content could be either compatible (green) or incompatible (purple) with the direction of the intervening mouse movement action. The proportion of compatible to incompatible trials was manipulated across blocks of the experiment.

151 **Behavioral task stimuli and procedure**

152 The behavioral task (**Fig. 1b**) was nearly identical to that used by Miller et al. (2020;
153 Experiment 1), and the description below recapitulates those methods. The task was
154 programmed and presented using MATLAB (<https://www.mathworks.com/>), running
155 Psychtoolbox routines (Brainard, 1997; <http://psychtoolbox.org/>), along with custom
156 scripts to continuously track mouse positions. Stimuli were displayed on a neutral grey
157 background (RGB: [128,128,128]) and viewed from approximately 60 cm. The WM
158 stimuli consisted of directional words ('up,' 'down,' 'left,' or 'right') that were displayed in
159 black lettering. Every trial began with a 2 sec intertrial interval (ITI). Then a WM sample
160 word appeared centrally for 1 sec. After a total delay of 5 sec, a WM probe word
161 (selected from the same set as the WM samples) appeared centrally underneath a
162 question mark. The WM task was to make a keyboard button press with the left hand
163 indicating whether the probe word was a match ('S' key) or non-match ('D' key) to the

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164 WM sample. Match and non-match WM probes were equally likely (50% match / 50%
165 non-match) and occurred in random order.

166 During the WM delay, participants completed a cued hand movement. A central
167 filled colored square (i.e., the cue) was flanked by unfilled square boxes (i.e., the
168 targets) at each of four locations: to the top, bottom, left, and right of center. The central
169 square could be one of four colors (RGB: green = [122,164, 86], pink = [198, 89, 153],
170 orange = [201,109, 68], blue = [119,122, 205]), which were chosen to be maximally
171 distinct, matched on saturation and brightness, and color-blind friendly
172 (<http://tools.medialab.sciences-po.fr/iwanthue/>). Each color was instructed to cue one of
173 four screen locations: green = *left*, pink = *right*, orange = *up*, blue = *down*. The target
174 boxes were equidistant from the central color cue and from each other (~3.7° in size,
175 ~9.3° in distance from center). The motor task was to move the mouse with the right
176 hand and click inside the target box at the location cued by the color. The motor task
177 therefore required a symbolic transformation from color to location, which was meant to
178 engage the goal representation circuitry involved in gating motor behaviors (Oliveira &
179 Ivry, 2008; O'Reilly & Frank, 2006). The motor task epoch ended when a 2 sec
180 response deadline passed.

181 Together, the sequence of one complete dual-task trial started with a 2 sec ITI,
182 followed by a 1 sec WM sample display, then a 2 sec fixation delay. After this first delay,
183 the motor task display appeared for 2 sec, followed by another fixation delay of 1 sec,
184 and then finally the WM probe display for 2 sec. In the main departure from a previous
185 version of the task (Miller et al., 2020), trial timing was fixed to ensure a consistent task
186 duration, in the effective TMS window, for each participant and session regardless of
187 response time. There were two primary trial types: compatible trials, wherein the
188 meaning of the WM word matched the cued direction of movement, and incompatible
189 trials, wherein the WM word was paired with any of the three non-matching movement
190 cues. The ratio of compatible to incompatible trials was manipulated across a given task
191 block. Blocks contained either 80%, 50%, or 20% compatible trials. In “high
192 compatibility” blocks (80% compatible), the WM sample would usually help the motor
193 task, as it suggested the goal direction for the upcoming movement. In “middle
194 compatibility” blocks (50% compatible), the WM content was equally likely to help or
195 harm to the motor task on any given trial. In “low compatibility” blocks (20% compatible)
196 the WM sample meaning usually differed from the motor task target, and was therefore
197 unhelpful. To minimize variability across participant learning effects, they were explicitly
198 informed about the percentage of compatible trials at the start of each block.

199 Participants practiced at least 12 trials of the motor task, to learn the color-direction
200 response mapping to criterion, before the first experimental session. In all sessions,
201 participants completed one 5-trial practice block of each dual-task block condition (15
202 total practice trials, with feedback for motor and WM response accuracy) before

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203 completing three 30-trial experimental blocks of each condition (9 blocks total; without
204 feedback). Participants therefore completed 90 trials in each block condition and 135
205 trials of each compatibility condition across blocks (72 incompatible/18 compatible trials
206 across “low compatibility” blocks, 45 incompatible/45 compatible trials across “middle
207 compatibility” blocks, and 18 incompatible/72 compatible trials across “high
208 compatibility” blocks). This amounted to 270 total trials per subject in each session, and
209 810 total trials per subject across sessions. The first block in each session was always
210 middle compatibility (50% compatible) and the predictability conditions occurred in
211 random order for the remaining blocks. The difference in motor behavior on compatible
212 vs. incompatible trials—or the ‘compatibility effect’—will serve here as an operational
213 index of the WM influence over ongoing action.

214

215 ***MRI methods***

216 **Acquisition**

217 All images were acquired on a research-dedicated Siemens TIM/Trio 3T MRI
218 system in the Henry H. Wheeler, Jr. Brain Imaging Center at the University of California,
219 Berkeley. High-resolution anatomical images were acquired with a T1-weighted
220 MPRAGE sequence (TR: 2300ms; TE: 2.98ms; flip angle: 9°; 160 sagittal slices; 1 × 1 ×
221 1 mm). After the anatomical scan, participants completed one run of closed-eye rest for
222 9-10 minutes. Functional pulse sequence parameters varied slightly across participants,
223 as some were recruited from other studies within the lab. That is, we already had the
224 necessary scans on file for some participants. The resting functional data are
225 inessential to the main conclusions and are included only in exploratory analyses.
226 Functional data were acquired with a gradient echo T2*-weighted echo-planar imaging
227 (EPI) sequence (*15 subjects* - TR: 2000ms, TE: 23ms, flip angle: 50°, 35 transverse
228 slices, 3 × 3 × 3 mm; *6 subjects* - TR: 2000ms, TE: 32.2ms, flip angle: 45°, 54
229 transverse slices, 2.5 × 2.5 × 2.5 mm; *3 subjects* - TR: 2000ms, TE: 28ms, flip angle:
230 78°, 32 transverse slices, 3 × 3 × 3 mm).

231

232 **Analysis**

233 *TMS target transformation*

234 The target Montreal Neurological Institute (MNI) coordinates were first converted
235 into each participants’ native space for TMS. Each participant’s T1-weighted anatomical
236 MRI was passed through the *SPM12* normalization procedure
237 (<https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>) to the MNI template space
238 (*normalise* function). The affine transformation mapping was then used to derive the
239 individual native space coordinates that corresponded to the MNI coordinates of the *a*
240 *priori* target ([-40, 32, 32]).

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241 *fMRI preprocessing*

242 Exploratory results included in this manuscript come from preprocessing performed
243 using *fMRIPrep* 1.4.0 (Esteban et al., 2019; RRID:SCR_016216), which is based
244 on *Nipype* 1.2.0 (Gorgolewski et al., 2017; RRID:SCR_002502).

245

246 *Resting-state connectivity analysis*

247 For each participant's fMRI resting-state timeseries, correlation was calculated
248 between the TMS target coordinate (5mm sphere) and all other brain voxels. To
249 calculate correlations, functional data were filtered between 0.01 and 0.1 Hz, detrended
250 and standardized, and the top 5 CompCor components were included as confound
251 regressors (implemented in *Nilearn* python package). A fixed-effects GLM across all
252 participants was then calculated in SPM12 to obtain the voxels with the highest overlap
253 with the target coordinate. The group connectivity map was then clustered in *Nilearn*
254 and the mean values for top clusters were extracted for each participant.

255

256 **TMS Methods**

257 **TMS design**

258 It is difficult to achieve perfect experimental control in TMS research. TMS over
259 different cortical targets can produce vastly different scalp sensations and degrees of
260 participant discomfort (Meteyard & Holmes, 2018). Apparent regional differences in
261 TMS response may further be driven by differences in scalp-to-cortex distance
262 (McConnell et al., 2001) or cortical geometry (Pell et al., 2011) that are unrelated to the
263 function of interest. Moreover, TMS to cortical sites of no experimental interest (which is
264 a common control condition) can propagate throughout networks that are involved in
265 task performance (Jung et al., 2016). These factors can disguise the ground truth and
266 obscure whether stimulation effects are driven by "control" or experimental TMS. Here,
267 we took two measures to achieve experimental control. First, we used two different
268 active TMS protocols (cTBS and iTBS), to the same experimental target site. Unlike
269 sham TMS or control stimulation to a different region — which would both produce
270 noticeably different sensations from the experimental stimulation — cTBS vs. iTBS
271 provide strong active controls for each other. Both protocols deliver the same number of
272 pulses, in bursts of the same frequency, at the same intensity, to the same target
273 region. However, because of differences in the patterning of bursts, the protocols are
274 expected to have opposite effects on cortical excitability (Huang et al., 2005). The
275 different forms of stimulation should therefore produce distinct outcomes in behaviors
276 that depend on the targeted region. Second, we supplemented this active control with a

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277 no-TMS condition (where all other procedures were identical), to replicate previous
278 findings and establish the ground truth performance on each task measure.

279

280 **Target selection**

281 Here, we aimed to interrogate the mechanisms that prioritize and deploy WM
282 content for action. The selection and use of WM, or ‘output gating’, has been attributed
283 to a cortico-striatal pathway, specifically to connectivity between the lateral PFC and
284 caudate nucleus (Chatham et al., 2014). We therefore aimed to stimulate this cortico-
285 striatal circuit. We cannot directly target subcortex with TMS, but TMS to the mid-lateral
286 PFC can selectively modulate dopamine synthesis and fMRI activity in the caudate, as
287 compared to more caudal PFC TMS which modulates the putamen (Riddle et al., 2022;
288 Schouwenburg et al., 2012; Strafella et al., 2001, 2003). That is, TMS to distinct frontal
289 cortical targets, with distinct anatomical connectivity profiles, can alter fMRI and
290 neuromodulatory activity in select subcortical nuclei. This sort of ‘sling-shot’ approach
291 has also been reliably applied to cortical temporal and parietal targets to modulate
292 hippocampal activity and memory performance (Tambini et al., 2018; Wang et al.,
293 2014). We chose a left dorsal mid-lateral PFC target region [MNI: -40, 32, 32] with
294 demonstrated anatomical and functional connectivity to striatum, using peak
295 coordinates from prior studies that have been shown to modulate caudate activity in
296 response to TMS (Choi et al., 2012; Petrides et al., 1993; Strafella et al., 2001; **Fig. 1a**).
297 We reasoned that this PFC target would be most likely to engage the circuitry that is
298 relevant to our cognitive functions of interest.

299

300 **TMS equipment and parameters**

301 A Magstim Super Rapid stimulator with two booster modules delivered stimulation
302 via a Magstim Double 70mm Air Film coil. We used theBrainsight 2 frameless
303 stereotactic neuronavigation system (Rogue Research, Montreal, Canada) to localize
304 the TMS targets for each participant and to monitor the coil position throughout each
305 stimulation run. The coil was oriented perpendicular to the underlying gyral/sulcal
306 anatomy, and the coil handle was positioned posterior to the coil head.

307 To individually calibrate the stimulation intensity for each participant, we assessed
308 motor threshold (MT) using electromyographic recording of the dorsal interosseus
309 muscle of the right hand. Single pulses were delivered over the hand representation
310 area of left primary motor cortex, which was first approximated as 5cm lateral from the
311 vertex. Then a search procedure, moving along a grid around that spot, identified the
312 location where stimulation produced the greatest motor-evoked potential (MEP) when
313 the muscle was relaxed. This was defined as the motor “hot spot.” The hot-spot was
314 then used to measure active motor threshold: the minimum single-pulse stimulation

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315 intensity required to produce 5 out of 10 MEPs, with peak-to-peak amplitude of at least
316 200 μ V, while the participant maintained a voluntarily muscle contraction of ~20%. A raw
317 EMG display provided the participant with continuous visual feedback to facilitate
318 consistent force of muscle contraction. Active MT ranged from 36-65 percent of
319 maximum stimulator output (mean: 45.2) across this sample.

320 Following published procedures and safety guidelines (Oberman et al., 2011), the
321 stimulation intensity was set at 80% of each participant's active motor threshold.
322 However, we had difficulty reaching a stable threshold for two participants. At high
323 stimulation intensities we observed occasional large MEPs, but few twitches in the
324 contralateral finger and few MEPs within the specified thresholding range. In order to
325 preserve participant comfort and safety, we capped TBS intensity at 44% MSO.
326 Therefore, stimulation intensities ranged from 29-44% in this sample.

327 The two experimental TMS sessions delivered an offline theta-burst TMS protocol
328 (Huang et al., 2005), which can result in up to 60 min of impact on cortical excitability of
329 the targeted region (Gamboa et al., 2010; Gentner et al., 2008; Grossheinrich et al.,
330 2009). Theta-burst stimulation (TBS) comprises trains of 3 pulses at 50 Hz, delivered
331 once every 200 msec (i.e., at theta frequency). TBS is delivered in two primary patterns:
332 continuous TBS (cTBS) and intermittent TBS (iTBS). cTBS involves a continuous train
333 of TBS for a total duration of 40 sec, whereas iTBS involves 2 sec trains of TBS
334 repeated every 10 seconds (i.e., with an 8 sec break between trains), for a total of 190
335 seconds. Both cTBS and iTBS protocols deliver a total of 600 pulses. Whereas cTBS
336 has been found to produce transient decreases in cortical excitability, iTBS is instead
337 associated with transient increases in excitability. Moreover, these protocols, delivered
338 to the same frontal region, have shown distinct effects on striatal dopamine release
339 (Aceves-Serrano et al., 2022). While individuals are variable in their degree and
340 direction of TMS effects (Cantone et al., 2019; Corp et al., 2020; Hamada et al., 2013;
341 Tik et al., 2023), cTBS and iTBS are generally expected to have distinct effects on
342 cortical excitability when applied over the same cortical region. This experimental
343 design should therefore produce distinct behavioral effects of the stimulation conditions,
344 if the behavior depends on the lateral PFC target.

345 For each TMS session, participants first completed 15 trials of behavioral task
346 practice immediately before stimulation, then underwent the TBS procedure. One
347 experimenter delivered the stimulation while another monitored the participant for
348 comfort and safety. We observed facial twitching during stimulation in 5 (out of 24)
349 participants, but no participants reported pain and we observed no other adverse
350 effects. When the TBS protocol ended, participants rested for 5 minutes before
351 completing the behavioral task, which lasted 48 minutes.

352

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354 **Analysis strategy**

355 *Movement trajectory measures:* We continuously tracked the mouse position across
356 each trial of the motor task (**Fig. 2**). To evaluate the precision of motor trajectories, we
357 defined a circular boundary around the central start position, with a radius of $\frac{1}{4}$ the
358 distance to the target (**Fig. 2b**), and we measured the angle at which the cursor crossed
359 that boundary. We calculated the deviation from the target direction, and **Fig. 2a** shows
360 the distribution of these angular errors for all compatible and incompatible trials. To
361 quantify trajectories that initially curved away from the target location, movements were
362 considered precise if they first crossed the circular boundary within 45° of the correct
363 response axis, but were classified as course adjustments if they crossed the boundary
364 at a wider angle than 45° before terminating at the correct target (**Fig. 2b**). All cursor
365 trajectories were rotated to a common axis for comparison.

366 *Movement speed measures:* Movement initiation—also sometimes referred to as
367 ‘reaction time’—was defined as the time from the onset of the color cue until the cursor
368 first crossed a radius of 30 pixels from the starting position (**Fig. 2b**). Movement
369 duration—also sometimes referred to as ‘movement time’—was defined as the amount
370 of time after movement initiation until a click was made in any target box.

371 QA: For all experiments and measures, we excluded trials that were missing a WM
372 probe response. For movement speed analyses, we excluded outlier trials when a
373 measurement was greater than 3 standard deviations away from the participants’ mean,
374 or if the motor task response landed at the incorrect target location.

375 *Statistics:* We specified two sets of mixed-effects models to test the TMS influence
376 on WM-motor compatibility effects and block-level control. First, we used a set of ‘three-
377 target’ models that included the *no TMS* condition, so that both experimental TMS
378 conditions could be compared to ground truth behavior. We constructed linear models
379 with the response time variable of interest (e.g., movement initiation, movement
380 duration) as the outcome measure, and we coded predictor variables as PFC *TMS*
381 *protocol* (treatment coded with the *no TMS* condition as the relative baseline), *trial*
382 *compatibility* (compatible vs. incompatible), *block proportion* (continuous measure of
383 compatibility proportion for each block, mean-centered), and *block number* (mean-
384 centered), including interactions. For WM or movement accuracy, we used a logistic
385 mixed model with the same predictor variable coding. All mixed linear models were
386 constructed with subject as a random effect (random-intercepts), and built and tested
387 via the *lme4* (<https://github.com/lme4/lme4/>) and *lmerTest* (<https://rdrr.io/cran/lmerTest/>)
388 R packages, ported in Python via ryp2 (<https://rpy2.github.io/>).

389 We then constructed ‘two-target’ models with the same structure, but including only
390 the active TMS conditions. These were designed to directly compare cTBS vs. iTBS and
391 account for non-specific effects of stimulation. Both two- and three-target models reveal

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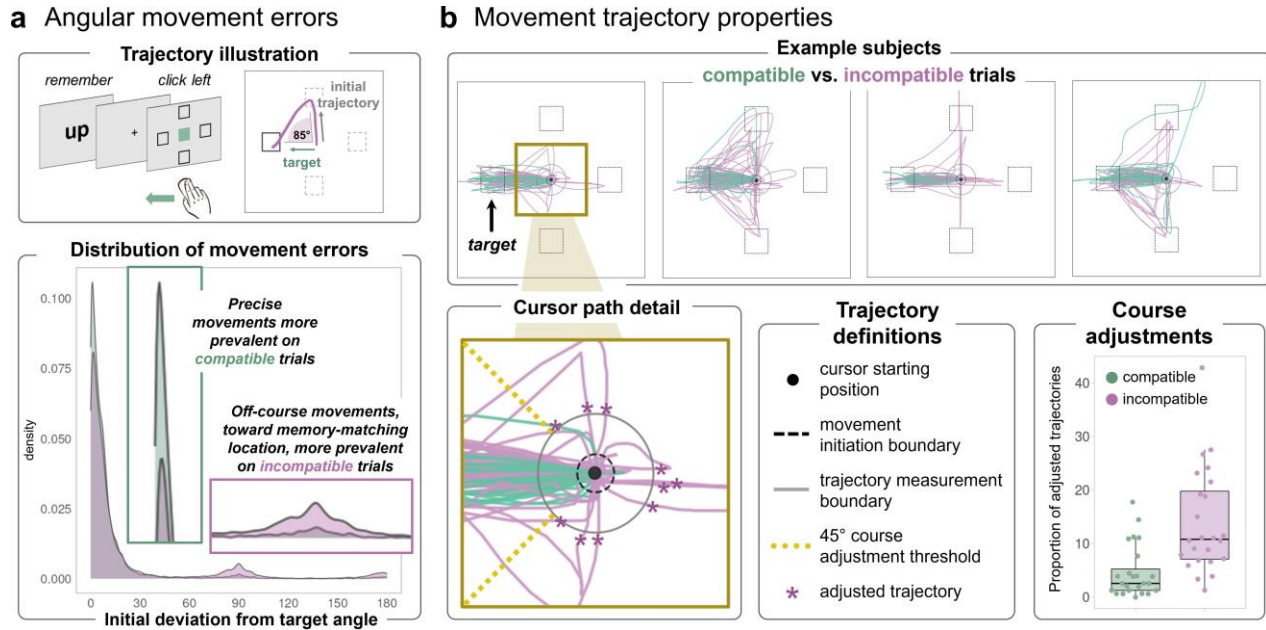


Figure 2. Dissecting discrete properties of movement behavior. (a) We continuously tracked mouse trajectories after the onset of the color movement cue. We calculated the initial deviation away from the target location, and display the frequency distribution of angular errors, for compatible and incompatible trials. (b) Movement trajectories for compatible (green) and incompatible trials (purple) from example subjects, in middle compatibility blocks (rotated to a common target direction). Detail illustrates boundaries for determining movement initiation, measuring angular error, and categorizing trials as course adjustments. Course adjustments were more frequent on incompatible trials (shown for middle compatibility blocks, when compatible and incompatible trials occurred equally often).

392 generally consistent outcomes, so are included to convey a full picture of the conditions
393 that drive significant effects. In visualizations we include the *no TMS* baseline alongside
394 the experimental TMS conditions, but conclusions are based on findings that differ
395 between the two experimental TMS conditions (cTBS and iTBS in the two-target model).

396 We also specified a final set of models to test the TMS influence on trial
397 compatibility sequence effects – that is, the influence of the preceding trial condition on
398 current trial compatibility effects. We selected only the neutral/middle compatibility block
399 conditions (block compatibility = 50%) from each session and coded an additional
400 variable for *previous trial compatibility* (compatible vs. incompatible). In these models,
401 PFC TMS protocol (either 3- or 2- way coded as above), *current trial compatibility*, and
402 *previous trial compatibility* were included as explanatory variables.

403 For the fixed effects of each model, we report a parameter estimate value,
404 estimated confidence interval (t-tests from *lmerTest* using Satterthwaite's approximation
405 (Kuznetsova et al., 2017)), and *p*-value. Full model specifications and fitting results are
406 listed in *Extended Data Tables*.

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410 **Results**

411 ***Baseline condition replicates previous findings***

412 We first aimed to replicate our previous behavioral findings, so we applied the prior
413 study analysis strategy (Miller et al., 2020) to the data from the *no TMS* condition here.
414 This was meant to ensure that basic WM-motor effects are reliable across studies and
415 cohorts. For all replication analyses, we conducted 2 (*trial compatibility*: compatible vs.
416 incompatible) × 3 (*block proportion compatible*: high vs. middle vs. low) repeated
417 measures ANOVAs, to mirror the previous study.

418 Motor decision accuracy (i.e., % correct of click location) was slightly worse on
419 incompatible (98%) vs. compatible trials (99%), $F(1,23) = 22.83$, $p < .001$, $\eta_p^2 = .18$, but
420 there was neither a main effect of *block proportion*, $F(2,46) = 1.4$, $p = .25$, $\eta_p^2 = .02$, nor
421 an interaction between factors, $F(2,46) = .11$, $p = .89$, $\eta_p^2 = .001$. When the meaning of
422 the WM content was incompatible with motor goals, participants chose the wrong target
423 location more often. Throughout the manuscript, we refer to this difference between
424 compatible and incompatible conditions as the 'compatibility effect'.

425 Movement landing positions were overall highly accurate (98% correct), but WM
426 content may bias the shape of movement trajectories. For instance, incompatible trials
427 may result in curved paths that are skewed toward the direction that matches the
428 meaning of the WM sample. Indeed, the proportion of movement course adjustments
429 was ~10% greater on incompatible versus compatible trials across all block conditions,
430 $F(1,23) = 33.71$, $p < .001$, $\eta_p^2 = .41$ (**Fig. 2b**). There was no effect of *block proportion*
431 condition ($p = .2$), but there was an interaction between *trial* and *block* factors $F(2,46) =$
432 7.76 , $p = .001$, $\eta_p^2 = .033$. Action slips on incompatible trials were especially likely in
433 high compatibility blocks when WM content was most likely to match movement goals.

434 WM content or its relevance to the motor task could influence multiple ongoing
435 processes. We therefore examined distinct *movement initiation* and *duration* measures
436 geared to index motor decision-making vs. movement execution speed, respectively. A
437 main effect of *trial compatibility*, $F(1,23) = 45.26$, $p < .001$, $\eta_p^2 = .35$, indicated that
438 movements were *initiated* more slowly when the cued movement was incompatible with
439 the WM sample meaning (67 ms difference). A main effect of *block proportion*, $F(2,46) =$
440 17.16 , $p < .001$, $\eta_p^2 = .15$, indicated that movements were also initiated more quickly
441 overall in blocks when WM content was more likely to help motor performance.
442 Moreover, there was an interaction between *trial compatibility* and *block proportion*
443 factors, $F(2,46) = 3.37$, $p = .043$, $\eta_p^2 = .016$, whereby the compatibility effect was
444 amplified in blocks with more compatible trials. Compatible movement initiation was
445 especially speeded when those trials were most likely (**Fig. 3a**).

446 *Movement duration* also showed a main effect of *trial compatibility*, $F(1,23) = 26.95$,
447 $p < .001$, $\eta_p^2 = .22$. Movements took longer on incompatible trials (38 msec difference).

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448 However, unlike movement *initiation* — which was overall speeded by a higher
 449 frequency of compatible trials — movement *duration* was slowed instead. There was an
 450 interaction between *trial* and *block* factors, $F(2,46) = 12.34$, $p < .001$, $\eta_p^2 = .067$, where
 451 the compatibility effect was amplified in blocks with more compatible trials. Incompatible
 452 movement duration was especially slowed when those trials were least likely (**Fig. 3b**).

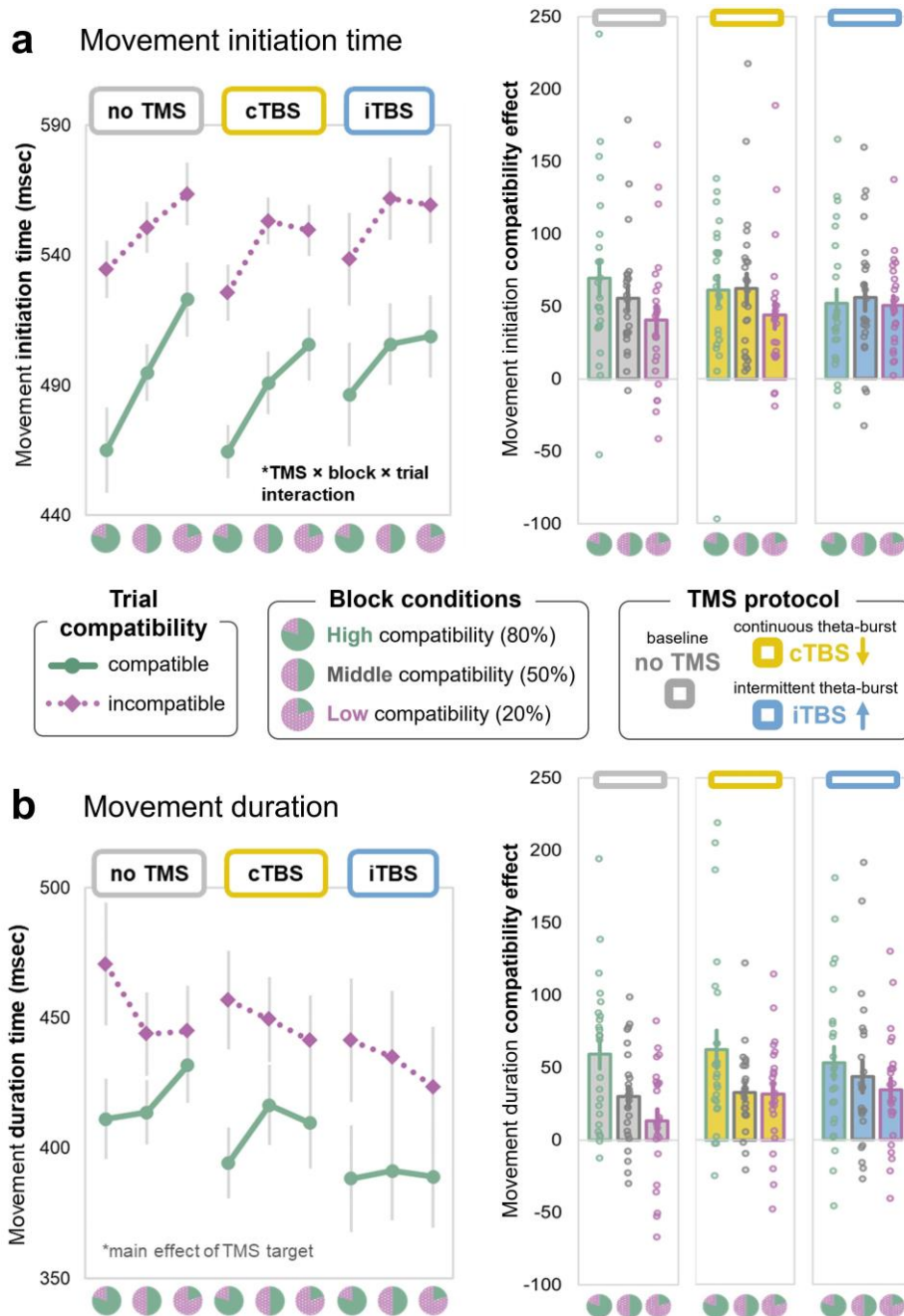


Figure 3. TMS effects on block-level cognitive control. Left panels illustrate raw group means for each TMS protocol, block proportion, and trial compatibility condition. Right panels illustrate compatibility effect difference scores (incompatible – compatible) for movement measures. (a) Movement initiation time. (b) Movement duration. Points reflect each individual subject average for that condition, and error bars reflect SEM.

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453 **Replication Summary:** These results show a near-identical replication of the
454 response pattern in our previous behavioral study, wherein motor benefits of compatible
455 WM content manifested in accelerated decision processes, while costs of incompatible
456 content manifested in more imprecise and time-consuming actions. Therefore, the *no*
457 *TMS* condition represents a stable baseline against which to compare behavior after
458 experimental TMS.

459

460 ***TMS influences block-level (proactive) cognitive control***

461 The replication analysis showed a systematic pattern of trial and block condition
462 effects, whereby the magnitude of compatibility effect was modulated by the likelihood
463 of compatible/incompatible trials: the greater the proportion of incompatible trials, the
464 less they impacted movement speed and accuracy. This pattern may be considered to
465 reflect sustained, anticipatory control over WM-action conflict at the level of the task
466 block context (i.e., proactive control; Braver, 2012). This pattern was altered after TMS
467 to mid-lateral PFC.

468 *Movement choice and trajectory:* In the original study, as well as our replication in
469 the *no TMS* condition, movement target choice accuracy was high, but displayed a
470 small compatibility effect. Here, TMS also produced an interaction with trial compatibility
471 and time across the task (i.e., block number, which was included in the model to capture
472 that neural effects of TMS are expected to decay over time). PFC-targeted cTBS
473 modulated the magnitude of compatibility effect across the course of the task relative to
474 a *no TMS* comparison ($\beta = 0.005$, $p = 0.044$), and in a direct iTBS vs. cTBS comparison
475 ($\beta = -0.005$, $p = 0.049$; see *Extd. Data Tables*). The compatibility effect (accuracy for
476 compatible vs. incompatible trials) was magnified after cTBS, especially in earlier task
477 blocks. This cTBS effect decreased over time, and there was no TMS interaction with
478 block proportion compatibility. TMS condition (either relative to *no TMS* or cTBS vs.
479 iTBS) also had no impact on the precision or course of correctly-chosen movements [*p-*
480 *values* > 0.2, see *Extd. Data*].

481 *Movement speed:* In the original study, and in the *no TMS* replication, movement
482 initiation was more conservative in blocks when incompatible trials were more likely.
483 Even compatible trial movements started slower in those blocks, suggesting a
484 temporally-extended tendency for response caution. Conversely, movement initiation
485 was overall speeded in blocks when incompatible trials were less likely, and this effect
486 was magnified for compatible trials, suggesting a lower movement decision threshold
487 when WM and movement goals tended to align. However, that block level (proactive)
488 modulation was attenuated after TMS (**Fig. 3a**). Movement initiation speed was
489 impacted by a combination of TMS target, block, and trial compatibility conditions (see
490 *Extd. Data Tables* for all tests), including a *TMS x trial compatibility x block proportion x*

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491 *block number* interaction in both models ($\beta = -26.4$ [CI: -44.8, -8], $p = 0.005$; 2-target
492 model), as well as a main effect of *TMS* protocol ($\beta = 13.8$ [CI: -6.4, 21.2], $p < 0.001$);
493 More specifically, after iTBS, there was no relative slowing when compatible trials were
494 least likely, and there was less benefit to compatible movement initiation when
495 compatible trials were most likely. Movement *duration*, however, showed no trial- or
496 block-type specific TMS effects. Instead, a graded effect of *TMS* protocol indicated that
497 movements were executed faster overall after iTBS (which is meant to be excitatory;
498 **Fig. 3b**) relative to both cTBS ($\beta = -18.6$ [CI: -26.7, -10.5], $p < 0.001$) and the *no TMS*
499 baseline ($\beta = -28.4$ [CI: -36.6, -20.2], $p < 0.001$).

500 *WM recognition*: WM probe accuracy was high overall, averaging 95-99% across all
501 TMS and task conditions, and unharmed by either stimulation condition. Both probe
502 accuracy and RT were worse on incompatible trials, but no other block or TMS effects
503 emerged in the two-target model (p -values > 0.2 , see *Extd. Data*). In fact, the three-
504 target model revealed that WM probe recognition was slightly more accurate on
505 incompatible trials after iTBS (compared to *no TMS* baseline: $\beta = 0.02$ [CI: 0.01, 0.03],
506 $p = 0.003$). Therefore, cognitive control in response to block-level trial proportions
507 seems to affect the intervening movement, but not memory performance. Moreover,
508 TMS seems to modulate the effect of WM on intervening movement behavior, without
509 harming the memory itself.

510 **Interim Summary**: Compatibility effects in movement choice accuracy were
511 amplified by cTBS to mid-lateral PFC, while trajectory precision was left unaffected.
512 TMS also modulated block-level (i.e., proactive) cognitive control over WM biases in
513 movement speed. iTBS impacted condition-specific control over movement initiation,
514 while movement duration showed a non-specific acceleration. iTBS seemed to eliminate
515 context-sensitive cognitive control settings that ignite or check movement initiation
516 depending on the relationship between internal content and action goals. These
517 condition-specific effects on movement choice and initiation time – but not trajectory
518 precision or movement duration – suggest that TMS modulated decision-making
519 processes, but not movement execution. WM probe accuracy remained high in all
520 conditions, indicating that TMS effects on conflict control are unlikely due to impacts on
521 the WM representation. Instead, the stimulated PFC region seems to uniquely modulate
522 the interplay between WM and actions, depending on their likelihood of overlap.

523

524 ***TMS influences trial-to-trial (reactive) cognitive control***

525 As shown above, TMS to lateral PFC modulates sustained cognitive control over
526 WM-motor interactions (as operationalized by block-level proportion compatibility
527 effects). In our previous study, we also delivered trial-level manipulations of item priority,
528 to examine control processes on a more immediate time scale. We found that
529 temporally-extended, higher-order task goals exerted distinct effects vs. phasic, item-

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530 level attentional modulation (Miller et al., 2020). We, therefore, reason that PFC may
531 make distinct contributions to block- vs. trial-level conflict control processes here
532 (Braver, 2012). ‘Congruency sequence effects’ describe a phenomenon observed in
533 conflict tasks like the Stroop or flanker, whereby the congruency effect on a given trial
534 interacts with the congruency condition of the preceding trial (Egner, 2007; Gratton et
535 al., 1992). Conflict effects tend to be magnified after a congruent trial, while they are
536 dampened after an incongruent trial – presumably because the conflict triggers a
537 reactive upregulation in cognitive control. Here, we extend this framework to illuminate
538 the principles of interplay between WM content and motor behavior. We examine the
539 effects of short-term context (i.e., the preceding trial) on WM-motor compatibility effects,
540 and test the contribution of lateral PFC to such a reactive, trial-by-trial form of WM-
541 action control. For these analyses, we focus only on middle compatibility task blocks
542 (50%), wherein compatible and incompatible trials occurred equally often.

543 *Movement choice and trajectory:* In the *no TMS* condition, movement accuracy
544 displayed a typical descriptive pattern of congruency sequence effects (**Fig. 4a**), but
545 many participants achieved 100% accuracy (and therefore showed no conditional
546 effects). There were no significant effects of previous trial compatibility or TMS condition
547 for either choice accuracy [*p-values* > 0.2], or course trajectory adjustments [*p-values* >
548 0.2, see *Extd. Data*].

549 *Movement speed:* In the *no TMS* condition, the sequence effects that are
550 characteristic of conflict scenarios (Egner, 2007) emerged here in trial-to-trial control
551 over WM-motor interactions. The movement initiation compatibility effect was smaller
552 following incompatible (vs. compatible) trials. Immediately after having experienced
553 incompatible trial conflict, compatible movements were initiated more slowly (relative to
554 when the preceding trial was compatible) while incompatible movements were initiated
555 more quickly (*current trial x previous trial compatibility* interaction; $\beta = -41.6$ [CI: -64.4, -
556 18.9], $p < 0.001$; **Fig. 4b**). This suggests that conflict between WM content and motor
557 goals triggered a control adjustment to dampen the influence of WM content (whether
558 helpful or harmful) on subsequent trials.

559 This distinctive marker of adaptive control was eliminated, and descriptively
560 reversed, after cTBS (*TMS x current trial x previous trial compatibility* interaction; three-
561 target model: $\beta = -43.7$ [CI: 11.7, 75.8], $p = 0.008$; two target model: $\beta = -39.3$ [CI: -
562 71.3, -7.2], $p = 0.016$). Movement initiation became overall slower after incompatible
563 trials, and the magnitude of compatibility effect was equivalent whether the previous trial
564 was compatible or incompatible (**Fig. 4b**). That is, rather than a reactive improvement to
565 incompatible responding after conflict (as would be expected under typical function),
566 movement initiation was delayed instead. This suggests that PFC cTBS interferes with
567 adaptive control that would otherwise enhance or dampen the influence of WM content
568 over movements, in response to compatible vs. incompatible trials respectively. Under

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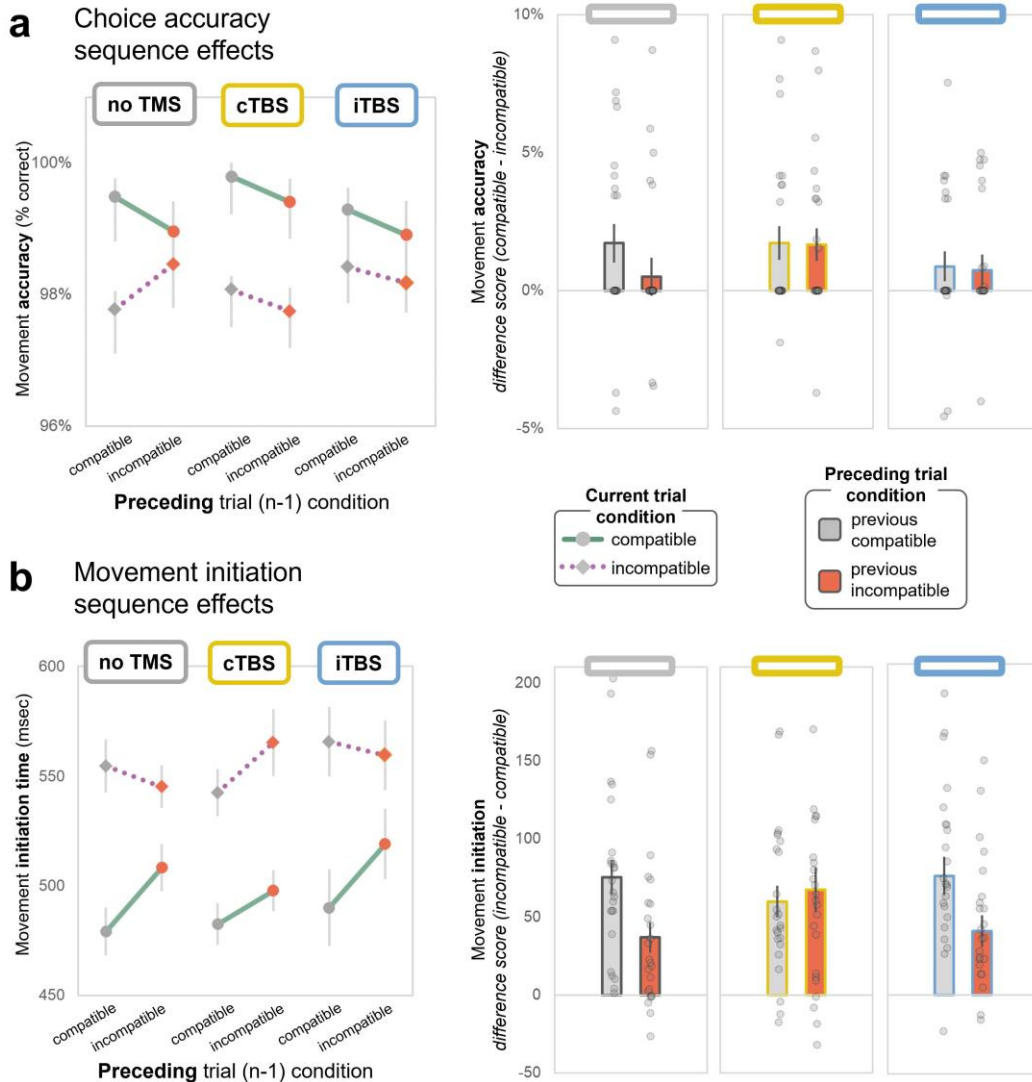


Figure 4. TMS effects on trial-by-trial compatibility sequence effects (CSE). CSE analyses were conducted only for middle compatibility blocks, wherein both trial types are equally likely. (a) Movement choice accuracy group means for each TMS condition, as a function of both current and previous trial compatibility (left). Different current trial compatibility conditions are displayed with separate lines, while previous (n-1) trial compatibility conditions are displayed with grey vs. red markers. Compatibility effect difference scores (compatible – incompatible) for each TMS and previous trial condition are shown on the right. (b) Movement initiation group means for each TMS condition, as a function of both current and previous trial compatibility (left). Compatibility effect differences scores (incompatible – compatible) for each TMS and previous trial condition are shown on the right. Points reflect each individual subject average for that condition, and error bars reflect SEM.

569 cTBS, incompatible movement initiation was especially hindered after incompatible
570 trials.

571 Movement duration displayed no such compatibility sequence effects and, like the
572 block-level control effects, PFC stimulation had no impact on trial-by-trial control over
573 movement duration [*p-values* > 0.2, see *Extd. Data*].

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574 **Interim Summary:** Conflict between dual-task WM content and action goals
575 displayed characteristic congruency sequence effects (in movement initiation time) and
576 TMS to mid-lateral PFC modulated this trial-by-trial control. cTBS, which is meant to be
577 inhibitory, eliminated the sensitivity to short-term control demands which is typically
578 expressed as a smaller compatibility effect after conflict trials. Instead, cTBS resulted in
579 overall slowing after incompatible trials, and a descriptively larger compatibility effect.
580 Choice accuracy effects failed to meet statistical thresholds, but descriptively mirrored
581 the pattern in movement initiation. Once again, TMS effects were limited to measures
582 that index decision processes. However, this reactive trial-by-trial control effect was
583 selectively modulated by cTBS, whereas the block-level control effects (in the previous
584 section) were modulated more by iTBS instead.

585

586 ***Exploratory analyses of individual variability***

587 This study was not powered to formally examine individual differences in behavior,
588 but it is now understood that TMS effects can vary widely with properties of the
589 individual, as well as their brain state (Corp et al., 2020; Silvanto et al., 2008; Silvanto &
590 Pascual-Leone, 2008). Connectivity between the targeted region and other task-
591 relevant areas may be an important explanatory factor in stimulation effects (Castrillon
592 et al., 2020). We therefore report some exploratory brain-behavior correlations to guide
593 future inquiry.

594

595 **Functional connectivity with the PFC target**

596 TMS effects are not confined to the targeted region, and instead can propagate
597 throughout a network (Eldaief et al., 2023; Hebscher & Voss, 2022). In fact, we hoped to
598 capitalize on this property to engage the cortico-striatal circuitry that is thought to
599 support the behavior we test here (Chatham et al., 2014; Strafella et al., 2001).
600 Moreover, cTBS and iTBS may be mediated by different connections, and induce
601 distinct physiological effects (Aceves-Serrano et al., 2022; Cocchi et al., 2015).
602 Therefore, we reasoned that the TMS effects observed here may further correlate with
603 the strength of individual functional connectivity between the targeted left lateral PFC
604 region and other putative control regions. Different connections may, moreover, be
605 important for different aspects of performance, namely proactive vs. reactive forms of
606 cognitive control. First, we identified regions that were most strongly correlated with the
607 TMS target site during resting-state fMRI (**Fig. 5a**). From that map, we then extracted
608 individual connectivity coefficients with regions-of-interest that are typically implicated in
609 WM and cognitive control – in this case, a parietal cluster and the dorsal medial PFC
610 (dmPFC, encompassing anterior cingulate cortex). We then correlated those

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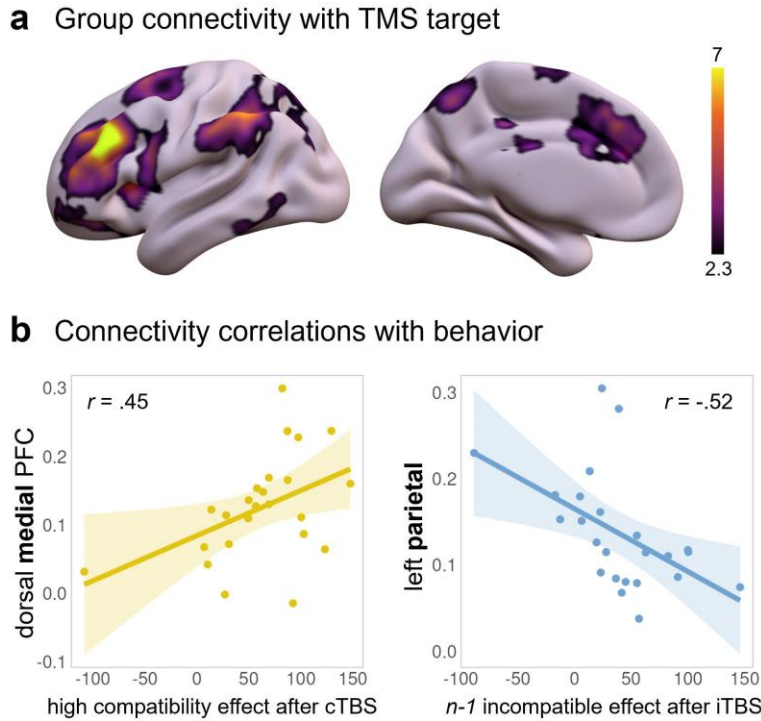


Figure 5. Resting state connectivity with TMS target site. (a) Group-level functional connectivity from the left lateral PFC seed region that was targeted with TMS. (b) Correlations between individual connectivity coefficients and behavioral metrics. Stronger connectivity with the dorsal medial PFC was associated with larger individual compatibility effects, in high compatibility blocks, after cTBS. Stronger connectivity with a left parietal cluster was associated with smaller compatibility effects, following incompatible trials, after iTBS.

611 connectivity metrics with measures of block- and trial-level cognitive control, which were
612 modulated by iTBS and cTBS respectively (**Fig. 5b**). We focused on compatibility
613 effects in movement initiation, since that measure was most consistently modulated by
614 TMS across analyses. We found that current trial compatibility effects after cTBS (but
615 not iTBS) correlated positively with dmPFC connectivity (Pearson's $r = .45$, $p = .027$),
616 but not with parietal ($r = -.26$, $p = .22$). That is, stronger connectivity between the TMS
617 target and dmPFC was associated with larger individual TMS-induced compatibility
618 effects (i.e., a marker of susceptibility to conflict). We also found that previous trial
619 compatibility effects after iTBS (but not cTBS) correlated negatively with parietal
620 connectivity ($r = -.52$, $p = .01$), but not with dmPFC ($r = -.05$, $p = .8$). That is, stronger
621 connectivity between the TMS target and the left parietal cluster was associated with
622 smaller TMS-induced compatibility effects after incompatible trials (i.e., a marker of
623 adaptive control). These are meant as only exploratory correlations, but they
624 corroborate the idea that cTBS and iTBS impacts on block- and trial-level control
625 measures may arise through distinct prefrontal circuits.

626

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627 **Discussion**

628 Here, we confirmed that verbal WM content can skew the speed and trajectory of
629 manual actions, indicating that WM may unintentionally shape ongoing movements.
630 However, this bias can be minimized when conflict between goals is predictable, so it is
631 also under a degree of strategic control. We then tested the role of left lateral PFC in
632 modulating this controlled interplay between WM and ongoing behavior. We perturbed
633 the region using two distinct TMS protocols (which should have different effects on
634 cortical excitability), and we examined the resultant effects on the type and magnitude
635 of WM-motor interactions. PFC TMS modulated indices of control over movement
636 choice accuracy and movement initiation time, but not movement trajectories or
637 duration. Moreover, iTBS dampened sensitivity to temporally-extended, block-level task
638 contingencies (i.e., proactive control), and cTBS dampened immediate, flexible
639 adaptation to trial-by-trial conflict (i.e., reactive control). Therefore, the same region of
640 left lateral PFC may implement both proactive and reactive forms of control over the
641 interplay between WM and actions, but may do so through different routes.

642

643 ***Adaptive control over conflict between WM and actions***

644 The behavior observed here resembles the effects of cognitive control in tasks like
645 the Stroop, flanker, or Simon, wherein prepotent stimulus and response tendencies may
646 be in conflict (Braem et al., 2019). The difference here is that the conflicting information
647 is not currently being perceived, but is maintained with WM instead. These findings
648 reaffirm a tight linkage between WM and motor behavior (van Ede, 2020), but now shed
649 light on the processes by which that linkage is controlled when multiple task goals vie
650 for priority.

651 We find that WM content can produce conflict in motor behavior much like
652 perceived stimuli do, and that interplay appears to follow similar control principles to
653 visual stimulus-response conflict. As in, WM-motor interactions are subject to both
654 proactive control in response to block-level compatibility contingencies, and reactive
655 control in response to recently experienced conflict. In both cases, however, WM
656 performance is unaffected by the control processes that regulate the motor bias. For
657 instance, WM probe accuracy is unaffected by block-level proportion compatibility,
658 suggesting that cognitive control does not suppress interfering WM content per se.
659 Control may instead act to differentiate or integrate WM and motor task sets depending
660 on their likelihood of overlap, while preserving WM integrity (Cole et al., 2017). For
661 instance, when WM and motor goals are likely to be compatible, the gate between them
662 might be open, promoting crosstalk, which would further facilitate compatible
663 movements. However, that crosstalk would also yield inadvertent spillover of WM
664 content into incompatible actions (cf. Hillman et al., 2024). In daily life, this might

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665 manifest as inappropriate keystrokes during typing, either because of a lax control state
666 or a high degree of overlap between our ongoing thoughts and typing goals.

667

668 ***Mid-lateral PFC contributions to memory, decision, and action processes***

669 PFC TMS modulated cognitive control over WM-motor interactions. TMS left WM
670 content recognition unharmed, and resulted in a general speeding of action execution
671 and WM probe responses. However, block- and trial-type specific TMS effects emerged
672 in choice and movement initiation time measures that likely index decision processes.
673 That is, rather than affecting memory or the movement itself, PFC TMS selectively
674 influenced measures of cognitive control that facilitate or limit the sway of WM content
675 on motor decisions. Lateral PFC, therefore, likely mediates the WM-motor
676 transformation instead of underpinning either WM or movement components alone. This
677 is consistent with findings that lateral PFC lesions or transient perturbation often leave
678 essential WM maintenance unharmed, but impair functions that involve manipulating or
679 otherwise controlling WM content (D'Esposito et al., 2006; D'Esposito & Postle, 1999;
680 Mackey et al., 2016). Here, PFC may enable prioritized WM content to bias evidence
681 accumulation for motor decision-making, whereas that decision-making is postponed
682 when WM content is less relevant (Shushruth et al., 2022). We targeted only a mid-
683 lateral PFC node associated with WM output gating. However, targeting a more caudal
684 fronto-putamen circuit might be expected to influence control over movement duration
685 or trajectory instead (Landau et al., 2009).

686

687 ***Mid-lateral PFC contributions to sustained vs. responsive adaptive control***

688 The targeted PFC region is also considered a processing nexus, with diverse
689 response properties and projections (Chaudhuri et al., 2015; Dang et al., 2021; Duncan,
690 2001; Miller & Fusi, 2013; Wang et al., 2023; Wasmuht et al., 2018), that coordinates
691 between abstract task goals and immediate concrete action plans (Nee & D'Esposito,
692 2016). By changing the excitability of the target region, TMS may shift the timescale of
693 PFC processing or alter connectivity with network regions that support more or less
694 temporally abstracted levels of control (Badre & Nee, 2018; Soltani et al., 2021; Soltani
695 & Koechlin, 2022). iTBS, which is meant to be excitatory, interfered with anticipatory
696 control that happens over a longer timescale — eliminating both costs and benefits that
697 depend on higher-order task contingencies. cTBS, which is meant to be inhibitory,
698 instead dampened responsive control that happens over a shorter timescale —
699 eliminating reactive conflict adaptation and subsequent control benefits. WM-related
700 PFC function is characterized by a trade-off between representational stability (which
701 may share mechanisms with proactive control) vs. flexible updating (which may have

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702 more in common with reactive control). Excitatory or inhibitory TMS may push the
703 scales in favor of a more stable or flexible prefrontal regime. When iTBS (presumably)
704 increases PFC excitability, it reduces protracted task stability, but when cTBS
705 (presumably) decreases PFC excitability, it reduces rapid task flexibility. This insight
706 could help reconcile competing takes on PFC coding schemes and activity dynamics
707 (e.g., Adam et al., 2023; Christophel et al., 2017; Constantinidis et al., 2018; Leavitt et
708 al., 2017; Lundqvist et al., 2018; Stokes, 2015; Stroud et al., 2024) in that they may, in
709 part, be a product of malleability in PFC control mode.

710

711 ***TBS effects are individually variable***

712 Here, we aimed to excite or inhibit a PFC-striatal circuit, but the downstream effects
713 of our stimulation are unknown. The directional effects of cTBS and iTBS can be widely
714 variable across people, and we cannot definitively link our outcomes to cortical
715 facilitation or inhibition. Nonetheless, the two protocols did evince distinct behavioral
716 outcomes in this sample, suggesting that they promoted distinct effects on neural
717 activity as intended. The two TMS protocols may have their influence by targeting
718 distinct prefrontal cell types, propagating through different connected regions, or
719 provoking distinct compensatory responses. Indeed, our exploratory brain-behavior
720 correlations indicate that behavioral metrics after cTBS and iTBS were associated with
721 unique functional connectivity profiles across individuals. Stronger dmPFC connectivity
722 was associated with heightened individual susceptibility to conflict after cTBS, while
723 stronger parietal connectivity was associated with dampened individual conflict
724 adaptation effects after iTBS. dmPFC is often implicated in conflict detection and
725 resolution (e.g., in Stroop and flanker tasks; Botvinick et al., 2004), while posterior
726 parietal cortex is implicated in maintaining recent trial history (e.g., Akrami et al., 2018).
727 Stronger connectivity with these control network regions might therefore facilitate
728 stronger relative TMS propagation or compensation depending on the current control
729 demands. More extensive examination of the PFC network pathways for different
730 timescales of WM-motor control, and tests of individual variability across a larger
731 sample should be fruitful areas for future inquiry.

732

733 ***Conclusions and implications***

734 Here, we tested a simple WM-motor interaction and found that the semantic
735 meaning of WM content biased intervening hand movements. WM can, therefore, hold
736 sway over ongoing motor behavior. Under typical PFC function, this interplay between
737 WM and actions is thermostatically regulated by changes in recent trial conflict history
738 as well as the conflict statistics of the overarching task context. Lateral PFC mediates

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739 both immediate (trial history) and overarching (block proportion compatibility) forms of
740 control to adaptively promote or prevent WM content from guiding actions. However,
741 perturbing normal PFC function may alter the balance between proactive and reactive
742 control. This suggests that the same PFC region supports distinct forms of control, but
743 through different network pathways, and changing PFC excitability can change the
744 timescale of control.

745

746

747

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750 A.K. and R01 MH063901 to M.D.

751

752 **Data and code availability**

753 Data and analysis code will be publicly shared in an OSF repository (<https://osf.io/jcytw/>)
754 upon publication.

755

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References

- Aceves-Serrano, L., Neva, J. L., Munro, J., Parent, M., Boyd, L. A., & Doudet, D. J. (2022). Continuous but not intermittent theta burst stimulation decreases striatal dopamine release and cortical excitability. *Experimental Neurology*, *354*, 114106. <https://doi.org/10.1016/j.expneurol.2022.114106>
- Adam, K. C. S., Rademaker, R. L., & Serences, J. T. (2023). Dynamics Are the Only Constant in Working Memory. *Journal of Cognitive Neuroscience*, *35*(1), 24–26. https://doi.org/10.1162/jocn_a_01941
- Akrami, A., Kopec, C. D., Diamond, M. E., & Brody, C. D. (2018). Posterior parietal cortex represents sensory history and mediates its effects on behaviour. *Nature*, *554*(7692), 368–372. <https://doi.org/10.1038/nature25510>
- Badre, D., & Nee, D. E. (2018). Frontal Cortex and the Hierarchical Control of Behavior. *Trends in Cognitive Sciences*, *22*(2), 170–188. <https://doi.org/10.1016/j.tics.2017.11.005>
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*(3), 624–652. <https://doi.org/10.1037/0033-295X.108.3.624>
- Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, *8*(12), 539–546. <https://doi.org/10.1016/j.tics.2004.10.003>
- Braem, S., Bugg, J. M., Schmidt, J. R., Crump, M. J. C., Weissman, D. H., Notebaert, W., & Egner, T. (2019). Measuring Adaptive Control in Conflict Tasks. *Trends in Cognitive Sciences*, *23*(9), 769–783. <https://doi.org/10.1016/j.tics.2019.07.002>
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. <https://doi.org/10.1163/156856897X00357>
- Braver, T. S. (2012). The variable nature of cognitive control: A dual mechanisms framework. *Trends in Cognitive Sciences*, *16*(2), 106–113. <https://doi.org/10.1016/j.tics.2011.12.010>
- Cantone, M., Lanza, G., Vinciguerra, L., Puglisi, V., Ricceri, R., Fiscaro, F., Vagli, C., Bella, R., Ferri, R., Pennisi, G., Di Lazzaro, V., & Pennisi, M. (2019). Age, Height, and Sex on Motor Evoked Potentials: Translational Data From a Large Italian Cohort in a Clinical Environment. *Frontiers in Human Neuroscience*, *13*. <https://www.frontiersin.org/articles/10.3389/fnhum.2019.00185>
- Carlisle, N. B., & Woodman, G. F. (2011). Automatic and strategic effects in the guidance of attention by working memory representations. *Acta Psychologica*, *137*(2), 217–225.
- Castrillon, G., Sollmann, N., Kurcyus, K., Razi, A., Krieg, S. M., & Riedl, V. (2020). The physiological effects of noninvasive brain stimulation fundamentally differ across the human cortex. *Science Advances*, *6*(5), eaay2739. <https://doi.org/10.1126/sciadv.aay2739>
- Chatham, C. H., Frank, M. J., & Badre, D. (2014). Corticostriatal Output Gating during Selection from Working Memory. *Neuron*, *81*(4), 930–942. <https://doi.org/10.1016/j.neuron.2014.01.002>
- Chaudhuri, R., Knoblauch, K., Gariel, M.-A., Kennedy, H., & Wang, X.-J. (2015). A Large-Scale Circuit Mechanism for Hierarchical Dynamical Processing in the Primate Cortex. *Neuron*, *88*(2), 419–431. <https://doi.org/10.1016/j.neuron.2015.09.008>

WORKING MEMORY BIASES ACTIONS

- Choi, E. Y., Yeo, B. T. T., & Buckner, R. L. (2012). The organization of the human striatum estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, *108*(8), 2242–2263. <https://doi.org/10.1152/jn.00270.2012>
- Christophel, T. B., Klink, P. C., Spitzer, B., Roelfsema, P. R., & Haynes, J.-D. (2017). The Distributed Nature of Working Memory. *Trends in Cognitive Sciences*, *21*(2), 111–124. <https://doi.org/10.1016/j.tics.2016.12.007>
- Cocchi, L., Sale, M. V., Lord, A., Zalesky, A., Breakspear, M., & Mattingley, J. B. (2015). Dissociable effects of local inhibitory and excitatory theta-burst stimulation on large-scale brain dynamics. *Journal of Neurophysiology*, *113*(9), 3375–3385. <https://doi.org/10.1152/jn.00850.2014>
- Cole, M. W., Braver, T. S., & Meiran, N. (2017). The task novelty paradox: Flexible control of inflexible neural pathways during rapid instructed task learning. *Neuroscience & Biobehavioral Reviews*, *81*, 4–15. <https://doi.org/10.1016/j.neubiorev.2017.02.009>
- Constantinidis, C., Funahashi, S., Lee, D., Murray, J. D., Qi, X.-L., Wang, M., & Arnsten, A. F. T. (2018). Persistent Spiking Activity Underlies Working Memory. *Journal of Neuroscience*, *38*(32), 7020–7028. <https://doi.org/10.1523/JNEUROSCI.2486-17.2018>
- Corp, D. T., Bereznicki, H. G. K., Clark, G. M., Youssef, G. J., Fried, P. J., Jannati, A., Davies, C. B., Gomes-Osman, J., Stamm, J., Chung, S. W., Bowe, S. J., Rogasch, N. C., Fitzgerald, P. B., Koch, G., Di Lazzaro, V., Pascual-Leone, A., & Enticott, P. G. (2020). Large-scale analysis of interindividual variability in theta-burst stimulation data: Results from the ‘Big TMS Data Collaboration.’ *Brain Stimulation*, *13*(5), 1476–1488. <https://doi.org/10.1016/j.brs.2020.07.018>
- Curtis, C. E., & D’Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. *Trends in Cognitive Sciences*, *7*(9), 415–423. [https://doi.org/10.1016/S1364-6613\(03\)00197-9](https://doi.org/10.1016/S1364-6613(03)00197-9)
- Dang, W., Jaffe, R. J., Qi, X.-L., & Constantinidis, C. (2021). Emergence of Nonlinear Mixed Selectivity in Prefrontal Cortex after Training. *Journal of Neuroscience*, *41*(35), 7420–7434. <https://doi.org/10.1523/JNEUROSCI.2814-20.2021>
- D’Esposito, M., Cooney, J. W., Gazzaley, A., Gibbs, S. E. B., & Postle, B. R. (2006). Is the prefrontal cortex necessary for delay task performance? Evidence from lesion and fMRI data. *Journal of the International Neuropsychological Society: JINS*, *12*(2), 248–260. <https://doi.org/10.1017/S1355617706060322>
- D’Esposito, M., & Postle, B. R. (1999). The dependence of span and delayed-response performance on prefrontal cortex. *Neuropsychologia*, *37*(11), 1303–1315. [https://doi.org/10.1016/S0028-3932\(99\)00021-4](https://doi.org/10.1016/S0028-3932(99)00021-4)
- Duncan, J. (2001). An adaptive coding model of neural function in prefrontal cortex. *Nature Reviews Neuroscience*, *2*(11), 820–829. <https://doi.org/10.1038/35097575>
- Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: Mental programs for intelligent behaviour. *Trends in Cognitive Sciences*, *14*(4), 172–179. <https://doi.org/10.1016/j.tics.2010.01.004>
- Egner, T. (2007). Congruency sequence effects and cognitive control. *Cognitive, Affective & Behavioral Neuroscience*, *7*(4), 380–390. <https://doi.org/10.3758/cabn.7.4.380>
- Eldaief, M. C., McMains, S., Izquierdo-Garcia, D., Daneshzand, M., Nummenmaa, A., & Braga, R. M. (2023). Network-specific metabolic and haemodynamic effects elicited by non-

WORKING MEMORY BIASES ACTIONS

- invasive brain stimulation. *Nature Mental Health*, 1(5), Article 5.
<https://doi.org/10.1038/s44220-023-00046-8>
- Esteban, O., Markiewicz, C. J., Blair, R. W., Moodie, C. A., Isik, A. I., Erramuzpe, A., Kent, J. D., Goncalves, M., DuPre, E., Snyder, M., Oya, H., Ghosh, S. S., Wright, J., Durnez, J., Poldrack, R. A., & Gorgolewski, K. J. (2019). fMRIPrep: A robust preprocessing pipeline for functional MRI. *Nature Methods*, 16(1), 111–116. <https://doi.org/10.1038/s41592-018-0235-4>
- Fuster, J. M. (2001). The prefrontal cortex--an update: Time is of the essence. *Neuron*, 30(2), 319–333.
- Gamboa, O. L., Antal, A., Moliadze, V., & Paulus, W. (2010). Simply longer is not better: Reversal of theta burst after-effect with prolonged stimulation. *Experimental Brain Research*, 204(2), 181–187. <https://doi.org/10.1007/s00221-010-2293-4>
- Gentner, R., Wankerl, K., Reinsberger, C., Zeller, D., & Classen, J. (2008). Depression of Human Corticospinal Excitability Induced by Magnetic Theta-burst Stimulation: Evidence of Rapid Polarity-Reversing Metaplasticity. *Cerebral Cortex*, 18(9), 2046–2053. <https://doi.org/10.1093/cercor/bhm239>
- Gorgolewski, K. J., Esteban, O., Ellis, D. G., Notter, M. P., Ziegler, E., Johnson, H., Hamalainen, C., Yvernault, B., Burns, C., Manhães-Savio, A., Jarecka, D., Markiewicz, C. J., Salo, T., Clark, D., Waskom, M., Wong, J., Modat, M., Dewey, B. E., Clark, M. G., ... Ghosh, S. (2017). *Nipype: A flexible, lightweight and extensible neuroimaging data processing framework in Python. 0.13.1* (Version 0.13.1) [Computer software]. Zenodo. <https://doi.org/10.5281/zenodo.581704>
- Gratton, G., H, G., & Donchin, E. (1992). Optimizing the use of information: Strategic control of activation of responses. *Journal of Experimental Psychology: General*, 121(4), 480–506. <https://doi.org/10.1037/0096-3445.121.4.480>
- Grossheinrich, N., Rau, A., Pogarell, O., Hennig-Fast, K., Reinl, M., Karch, S., Dieler, A., Leicht, G., Mulert, C., Sterr, A., & Padberg, F. (2009). Theta Burst Stimulation of the Prefrontal Cortex: Safety and Impact on Cognition, Mood, and Resting Electroencephalogram. *Biological Psychiatry*, 65(9), 778–784. <https://doi.org/10.1016/j.biopsych.2008.10.029>
- Hamada, M., Murase, N., Hasan, A., Balaratnam, M., & Rothwell, J. C. (2013). The Role of Interneuron Networks in Driving Human Motor Cortical Plasticity. *Cerebral Cortex*, 23(7), 1593–1605. <https://doi.org/10.1093/cercor/bhs147>
- Hebscher, M., & Voss, J. L. (2022). Transcranial Stimulation of Episodic Memory Networks. In E. M. Wassermann, A. V. Peterchev, U. Ziemann, S. H. Lisanby, H. R. Siebner, & V. Walsh (Eds.), *The Oxford Handbook of Transcranial Stimulation* (p. 0). Oxford University Press. <https://doi.org/10.1093/oxfordhb/9780198832256.013.33>
- Heinen, K., Feredoes, E., Ruff, C. C., & Driver, J. (2017). Functional connectivity between prefrontal and parietal cortex drives visuo-spatial attention shifts. *Neuropsychologia*, 99, 81–91. <https://doi.org/10.1016/j.neuropsychologia.2017.02.024>
- Hillman, H., Botthof, T., Forrence, A. D., & McDougale, S. D. (2024). Dissociable Codes in Motor Working Memory. *Psychological Science*, 35(2), 150–161. <https://doi.org/10.1177/09567976231221756>
- Huang, Y.-Z., Edwards, M. J., Rounis, E., Bhatia, K. P., & Rothwell, J. C. (2005). Theta Burst Stimulation of the Human Motor Cortex. *Neuron*, 45(2), 201–206. <https://doi.org/10.1016/j.neuron.2004.12.033>

WORKING MEMORY BIASES ACTIONS

- Jin, W., Nobre, A. C., & van Ede, F. (2020). Temporal Expectations Prepare Visual Working Memory for Behavior. *Journal of Cognitive Neuroscience*, 32(12), 2320–2332. https://doi.org/10.1162/jocn_a_01626
- Jung, J., Bungert, A., Bowtell, R., & Jackson, S. R. (2016). Vertex Stimulation as a Control Site for Transcranial Magnetic Stimulation: A Concurrent TMS/fMRI Study. *Brain Stimulation*, 9(1), 58–64. <https://doi.org/10.1016/j.brs.2015.09.008>
- Kiyonaga, A., & Egner, T. (2014). The Working Memory Stroop Effect When Internal Representations Clash With External Stimuli. *Psychological Science*, 25(8), 1619–1629. <https://doi.org/10.1177/0956797614536739>
- Kiyonaga, A., Egner, T., & Soto, D. (2012). Cognitive control over working memory biases of selection. *Psychonomic Bulletin & Review*, 19(4), 639–646. <https://doi.org/10.3758/s13423-012-0253-7>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Landau, S. M., Lal, R., O’Neil, J. P., Baker, S., & Jagust, W. J. (2009). Striatal Dopamine and Working Memory. *Cerebral Cortex*, 19(2), 445–454. <https://doi.org/10.1093/cercor/bhn095>
- Leavitt, M. L., Mendoza-Halliday, D., & Martinez-Trujillo, J. C. (2017). Sustained Activity Encoding Working Memories: Not Fully Distributed. *Trends in Neurosciences*, 40(6), 328–346. <https://doi.org/10.1016/j.tins.2017.04.004>
- Lee, T. G., & D’Esposito, M. (2012). The Dynamic Nature of Top-Down Signals Originating from Prefrontal Cortex: A Combined fMRI–TMS Study. *The Journal of Neuroscience*, 32(44), 15458–15466. <https://doi.org/10.1523/JNEUROSCI.0627-12.2012>
- Lundqvist, M., Herman, P., & Miller, E. K. (2018). Working Memory: Delay Activity, Yes! Persistent Activity? Maybe Not. *Journal of Neuroscience*, 38(32), 7013–7019. <https://doi.org/10.1523/JNEUROSCI.2485-17.2018>
- Mackey, W. E., Devinsky, O., Doyle, W. K., Meager, M. R., & Curtis, C. E. (2016). Human Dorsolateral Prefrontal Cortex Is Not Necessary for Spatial Working Memory. *Journal of Neuroscience*, 36(10), 2847–2856. <https://doi.org/10.1523/JNEUROSCI.3618-15.2016>
- McConnell, K. A., Nahas, Z., Shastri, A., Lorberbaum, J. P., Kozel, F. A., Bohning, D. E., & George, M. S. (2001). The transcranial magnetic stimulation motor threshold depends on the distance from coil to underlying cortex: A replication in healthy adults comparing two methods of assessing the distance to cortex. *Biological Psychiatry*, 49(5), 454–459. [https://doi.org/10.1016/S0006-3223\(00\)01039-8](https://doi.org/10.1016/S0006-3223(00)01039-8)
- Meteyard, L., & Holmes, N. P. (2018). TMS SMART – Scalp mapping of annoyance ratings and twitches caused by Transcranial Magnetic Stimulation. *Journal of Neuroscience Methods*, 299, 34–44. <https://doi.org/10.1016/j.jneumeth.2018.02.008>
- Miller, E. K., & Fusi, S. (2013). Limber Neurons for a Nimble Mind. *Neuron*, 78(2), 211–213. <https://doi.org/10.1016/j.neuron.2013.04.007>
- Miller, J. A., Kiyonaga, A., Ivry, R. B., & D’Esposito, M. (2020). Prioritized verbal working memory content biases ongoing action. *Journal of Experimental Psychology: Human Perception and Performance*, 46(12), 1443–1457. <https://doi.org/10.1037/xhp0000868>

WORKING MEMORY BIASES ACTIONS

- Morgan, H. M., Jackson, M. C., van Koningsbruggen, M. G., Shapiro, K. L., & Linden, D. E. J. (2013). Frontal and parietal theta burst TMS impairs working memory for visual-spatial conjunctions. *Brain Stimulation*, 6(2), 122–129. <https://doi.org/10.1016/j.brs.2012.03.001>
- Nee, D. E., & D'Esposito, M. (n.d.). Causal evidence for lateral prefrontal cortex dynamics supporting cognitive control. *eLife*, 6. <https://doi.org/10.7554/eLife.28040>
- Nee, D. E., & D'Esposito, M. (2016). The hierarchical organization of the lateral prefrontal cortex. *eLife*, 5. <https://doi.org/10.7554/eLife.12112>
- Oberman, L., Edwards, D., Eldaief, M., & Pascual-Leone, A. (2011). Safety of Theta Burst Transcranial Magnetic Stimulation: A systematic review of the literature. *Journal of Clinical Neurophysiology*, 28(1), 67–74. <https://doi.org/10.1097/WNP.0b013e318205135f>
- Oliveira, F. T. P., & Ivry, R. B. (2008). The Representation of Action: Insights From Bimanual Coordination. *Current Directions in Psychological Science*, 17(2), 130–135. <https://doi.org/10.1111/j.1467-8721.2008.00562.x>
- Olivers, C. N. L., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. *Trends in Cognitive Sciences*. <https://doi.org/10.1016/j.tics.2011.05.004>
- Olivers, C. N. L., & Roelfsema, P. R. (2020). Attention for action in visual working memory. *Cortex*, 131, 179–194. <https://doi.org/10.1016/j.cortex.2020.07.011>
- O'Reilly, R. C., & Frank, M. J. (2006). Making Working Memory Work: A Computational Model of Learning in the Prefrontal Cortex and Basal Ganglia. *Neural Computation*, 18(2), 283–328. <https://doi.org/10.1162/089976606775093909>
- Pan, Y., Han, Y., & Zuo, W. (2019). The color-word Stroop effect driven by working memory maintenance. *Attention, Perception, & Psychophysics*, 81(8), 2722–2731. <https://doi.org/10.3758/s13414-019-01780-x>
- Pell, G. S., Roth, Y., & Zangen, A. (2011). Modulation of cortical excitability induced by repetitive transcranial magnetic stimulation: Influence of timing and geometrical parameters and underlying mechanisms. *Progress in Neurobiology*, 93(1), 59–98. <https://doi.org/10.1016/j.pneurobio.2010.10.003>
- Petrides, M., Alivisatos, B., Evans, A. C., & Meyer, E. (1993). Dissociation of human mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing. *Proceedings of the National Academy of Sciences*, 90(3), 873–877. <https://doi.org/10.1073/pnas.90.3.873>
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, 139(1), 23–38. <https://doi.org/10.1016/j.neuroscience.2005.06.005>
- Riddle, J., Scimeca, J. M., Pagnotta, M. F., Inglis, B., Sheltraw, D., Muse-Fisher, C., & D'Esposito, M. (2022). A guide for concurrent TMS-fMRI to investigate functional brain networks. *Frontiers in Human Neuroscience*, 16. <https://doi.org/10.3389/fnhum.2022.1050605>
- Rigotti, M., Barak, O., Warden, M. R., Wang, X.-J., Daw, N. D., Miller, E. K., & Fusi, S. (2013). The importance of mixed selectivity in complex cognitive tasks. *Nature*, 497(7451), 585–590. <https://doi.org/10.1038/nature12160>
- Schouwenburg, M. R. van, O'Shea, J., Mars, R. B., Rushworth, M. F. S., & Cools, R. (2012). Controlling Human Striatal Cognitive Function via the Frontal Cortex. *Journal of Neuroscience*, 32(16), 5631–5637. <https://doi.org/10.1523/JNEUROSCI.6428-11.2012>

WORKING MEMORY BIASES ACTIONS

- Schwartz, M. F. (1995). Re-examining the Role of Executive Functions in Routine Action Production. *Annals of the New York Academy of Sciences*, 769(1), 321–336. <https://doi.org/10.1111/j.1749-6632.1995.tb38148.x>
- Shushruth, S., Zylberberg, A., & Shadlen, M. N. (2022). Sequential sampling from memory underlies action selection during abstract decision-making. *Current Biology*, 32(9), 1949–1960.e5. <https://doi.org/10.1016/j.cub.2022.03.014>
- Silvanto, J., Cattaneo, Z., Battelli, L., & Pascual-Leone, A. (2008). Baseline Cortical Excitability Determines Whether TMS Disrupts or Facilitates Behavior. *Journal of Neurophysiology*, 99(5), 2725–2730. <https://doi.org/10.1152/jn.01392.2007>
- Silvanto, J., & Pascual-Leone, A. (2008). State-Dependency of Transcranial Magnetic Stimulation. *Brain Topography*, 21(1), 1. <https://doi.org/10.1007/s10548-008-0067-0>
- Soltani, A., & Koehlin, E. (2022). Computational models of adaptive behavior and prefrontal cortex. *Neuropsychopharmacology*, 47(1), 58–71. <https://doi.org/10.1038/s41386-021-01123-1>
- Soltani, A., Murray, J. D., Seo, H., & Lee, D. (2021). Timescales of cognition in the brain. *Current Opinion in Behavioral Sciences*, 41, 30–37. <https://doi.org/10.1016/j.cobeha.2021.03.003>
- Soto, D., Heinke, D., Humphreys, G. W., & Blanco, M. J. (2005). Early, involuntary top-down guidance of attention from working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 31(2), 248.
- Soto, D., Hodsoll, J., Rotshtein, P., & Humphreys, G. W. (2008). Automatic guidance of attention from working memory. *Trends in Cognitive Sciences*, 12(9), 342–348. <https://doi.org/10.1016/j.tics.2008.05.007>
- Soto, D., & Humphreys, G. W. (2007). Automatic guidance of visual attention from verbal working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 33(3), 730.
- Stokes, M. G. (2015). “Activity-silent” working memory in prefrontal cortex: A dynamic coding framework. *Trends in Cognitive Sciences*, 19(7), 394–405. <https://doi.org/10.1016/j.tics.2015.05.004>
- Strafella, A. P., Paus, T., Barrett, J., & Dagher, A. (2001). Repetitive Transcranial Magnetic Stimulation of the Human Prefrontal Cortex Induces Dopamine Release in the Caudate Nucleus. *The Journal of Neuroscience*, 21(15), RC157–RC157. <https://doi.org/10.1523/JNEUROSCI.21-15-j0003.2001>
- Strafella, A. P., Paus, T., Fraraccio, M., & Dagher, A. (2003). Striatal dopamine release induced by repetitive transcranial magnetic stimulation of the human motor cortex. *Brain*, 126(12), 2609–2615. <https://doi.org/10.1093/brain/awg268>
- Stroud, J. P., Duncan, J., & Lengyel, M. (2024). The computational foundations of dynamic coding in working memory. *Trends in Cognitive Sciences*. <https://doi.org/10.1016/j.tics.2024.02.011>
- Tambini, A., Nee, D. E., & D’Esposito, M. (2018). Hippocampal-targeted Theta-burst Stimulation Enhances Associative Memory Formation. *Journal of Cognitive Neuroscience*, 1–21. https://doi.org/10.1162/jocn_a_01300
- Theeuwes, J., Belopolsky, A., & Olivers, C. N. L. (2009). Interactions between working memory, attention and eye movements. *Acta Psychologica*, 132(2), 106–114.

WORKING MEMORY BIASES ACTIONS

- Tik, M., Vasileiadi, M., Woletz, M., Linhardt, D., Schuler, A.-L., Williams, N., & Windischberger, C. (2023). Concurrent TMS/fMRI reveals individual DLPFC dose-response pattern. *NeuroImage*, 120394. <https://doi.org/10.1016/j.neuroimage.2023.120394>
- van Ede, F. (2020). Visual working memory and action: Functional links and bi-directional influences. *Visual Cognition*, 28(5–8), 401–413. <https://doi.org/10.1080/13506285.2020.1759744>
- van Ede, F., Chekroud, S. R., & Nobre, A. C. (2019). Human gaze tracks attentional focusing in memorized visual space. *Nature Human Behaviour*, 3(5), Article 5. <https://doi.org/10.1038/s41562-019-0549-y>
- Wang, J. X., Rogers, L. M., Gross, E. Z., Ryals, A. J., Dokucu, M. E., Brandstatt, K. L., Hermiller, M. S., & Voss, J. L. (2014). Targeted enhancement of cortical-hippocampal brain networks and associative memory. *Science*, 345(6200), 1054–1057. <https://doi.org/10.1126/science.1252900>
- Wang, W., Qi, M., & Gao, H. (2021). An ERP investigation of the working memory stroop effect. *Neuropsychologia*, 152, 107752. <https://doi.org/10.1016/j.neuropsychologia.2021.107752>
- Wang, Y., Royer, J., Park, B., Vos de Wael, R., Larivière, S., Tavakol, S., Rodriguez-Cruces, R., Paquola, C., Hong, S.-J., Margulies, D. S., Smallwood, J., Valk, S. L., Evans, A. C., & Bernhardt, B. C. (2023). Long-range functional connections mirror and link microarchitectural and cognitive hierarchies in the human brain. *Cerebral Cortex*, 33(5), 1782–1798. <https://doi.org/10.1093/cercor/bhac172>
- Wasmuht, D. F., Spaak, E., Buschman, T. J., Miller, E. K., & Stokes, M. G. (2018). Intrinsic neuronal dynamics predict distinct functional roles during working memory. *Nature Communications*, 9(1), 3499. <https://doi.org/10.1038/s41467-018-05961-4>

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Extended Data Tables

Three-target models (no TMS vs. cTBS vs. iTBS)

Table 1a. Movement choice accuracy

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.00	0.99 – 1.00	< 0.001
target [PFC_cTBS]	-0.00	-0.01 – 0.00	0.292
target [PFC iTBS]	-0.00	-0.01 – 0.00	0.334
TrialType2	-0.01	-0.02 – -0.01	< 0.001
BlockType_continuous_centered	0.00	-0.01 – 0.02	0.625
block_centered	0.00	-0.00 – 0.00	0.681
target [PFC_cTBS] : TrialType2	0.00	-0.01 – 0.01	0.776
target [PFC iTBS] : TrialType2	0.00	-0.00 – 0.01	0.531
target [PFC_cTBS] * BlockType_continuous_centered	0.00	-0.02 – 0.02	0.992
target [PFC iTBS] * BlockType_continuous_centered	0.01	-0.01 – 0.03	0.389
TrialType2 * BlockType_continuous_centered	-0.01	-0.03 – 0.02	0.624
target [PFC_cTBS] * block_centered	-0.00	-0.00 – 0.00	0.078
target [PFC iTBS] * block_centered	-0.00	-0.00 – 0.00	0.967
TrialType2 * block_centered	-0.00	-0.00 – 0.00	0.971
BlockType_continuous_centered * block_centered	-0.00	-0.01 – 0.01	0.865
(target [PFC_cTBS] * TrialType2) * BlockType_continuous_centered	-0.02	-0.05 – 0.01	0.149
(target [PFC iTBS] * TrialType2) * BlockType_continuous_centered	-0.02	-0.05 – 0.01	0.244
(target [PFC_cTBS] * TrialType2) * block_centered	0.00	0.00 – 0.01	0.044
(target [PFC iTBS] * TrialType2) * block_centered	0.00	-0.00 – 0.00	0.979
(target [PFC_cTBS] * BlockType_continuous_centered) * block_centered	0.00	-0.01 – 0.01	0.496
(target [PFC iTBS] * BlockType_continuous_centered) * block_centered	-0.00	-0.01 – 0.01	0.936
(TrialType2 * BlockType_continuous_centered) * block_centered	-0.00	-0.01 – 0.01	0.940
(target [PFC_cTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	0.00	-0.01 – 0.02	0.614
(target [PFC iTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	0.01	-0.01 – 0.02	0.263
Random Effects			
σ^2			0.01
τ_{00} subject			0.00
ICC			0.01
N subject			24
Observations			22391
Marginal R^2 / Conditional R^2			0.004 / 0.011

WORKING MEMORY BIASES ACTIONS

Table 1b. Movement trajectory precision

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	11.32	8.27 – 14.36	< 0.001
target [PFC_cTBS]	-0.97	-2.50 – 0.56	0.212
target [PFC iTBS]	-0.75	-2.28 – 0.79	0.340
TrialType2	10.30	8.75 – 11.86	< 0.001
BlockType_continuous_centered	-2.66	-7.13 – 1.82	0.244
block_centered	0.10	-0.31 – 0.52	0.633
target [PFC_cTBS] : TrialType2	1.96	-0.23 – 4.14	0.079
target [PFC iTBS] : TrialType2	1.29	-0.90 – 3.47	0.249
target [PFC_cTBS] * BlockType_continuous_centered	1.67	-4.66 – 8.01	0.605
target [PFC iTBS] * BlockType_continuous_centered	0.57	-5.79 – 6.93	0.861
TrialType2 * BlockType_continuous_centered	10.82	4.44 – 17.20	0.001
target [PFC_cTBS] * block_centered	0.20	-0.39 – 0.78	0.512
target [PFC iTBS] * block_centered	0.11	-0.47 – 0.69	0.721
TrialType2 * block_centered	0.46	-0.13 – 1.05	0.126
BlockType_continuous_centered * block_centered	0.43	-1.45 – 2.30	0.655
(target [PFC_cTBS] * TrialType2) * BlockType_continuous_centered	-2.37	-11.40 – 6.67	0.608
(target [PFC iTBS] * TrialType2) * BlockType_continuous_centered	2.19	-6.91 – 11.28	0.637
(target [PFC_cTBS] * TrialType2) * block_centered	0.14	-0.69 – 0.97	0.737
(target [PFC iTBS] * TrialType2) * block_centered	0.01	-0.82 – 0.84	0.987
(target [PFC_cTBS] * BlockType_continuous_centered) * block_centered	-1.69	-4.33 – 0.95	0.209
(target [PFC iTBS] * BlockType_continuous_centered) * block_centered	-0.95	-3.62 – 1.73	0.487
(TrialType2 * BlockType_continuous_centered) * block_centered	-0.92	-3.56 – 1.73	0.496
(target [PFC_cTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	1.04	-2.69 – 4.76	0.585
(target [PFC iTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	1.96	-1.84 – 5.76	0.313
Random Effects			
σ^2			885.35
τ_{00} subject			50.55
ICC			0.05
N subject			24
Observations			22125
Marginal R^2 / Conditional R^2			0.033 / 0.085

WORKING MEMORY BIASES ACTIONS

Table 1c. Movement initiation

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	492.91	472.47 – 513.36	< 0.001
target [PFC_cTBS]	-5.96	-13.43 – 1.51	0.118
target [PFC iTBS]	7.87	0.40 – 15.35	0.039
TrialType2	54.39	46.81 – 61.97	< 0.001
BlockType_continuous_centered	-97.73	-119.58 – -75.89	< 0.001
block_centered	-3.25	-5.28 – -1.21	0.002
target [PFC_cTBS] : TrialType2	1.54	-9.13 – 12.21	0.778
target [PFC iTBS] : TrialType2	-1.87	-12.55 – 8.81	0.731
target [PFC_cTBS] * BlockType_continuous_centered	27.83	-3.09 – 58.75	0.078
target [PFC iTBS] * BlockType_continuous_centered	48.11	17.06 – 79.15	0.002
TrialType2 * BlockType_continuous_centered	43.83	12.68 – 74.97	0.006
target [PFC_cTBS] * block_centered	-1.82	-4.68 – 1.04	0.213
target [PFC iTBS] * block_centered	2.01	-0.82 – 4.83	0.165
TrialType2 * block_centered	-0.58	-3.46 – 2.30	0.694
BlockType_continuous_centered * block_centered	15.75	6.60 – 24.91	0.001
(target [PFC_cTBS] * TrialType2) * BlockType_continuous_centered	-17.50	-61.60 – 26.60	0.437
(target [PFC iTBS] * TrialType2) * BlockType_continuous_centered	-26.59	-70.98 – 17.79	0.240
(target [PFC_cTBS] * TrialType2) * block_centered	0.79	-3.27 – 4.85	0.702
(target [PFC iTBS] * TrialType2) * block_centered	-2.13	-6.18 – 1.92	0.303
(target [PFC_cTBS] * BlockType_continuous_centered) * block_centered	-14.82	-27.71 – -1.94	0.024
(target [PFC iTBS] * BlockType_continuous_centered) * block_centered	-4.24	-17.29 – 8.81	0.524
(TrialType2 * BlockType_continuous_centered) * block_centered	-1.80	-14.71 – 11.10	0.784
(target [PFC_cTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	16.98	-1.20 – 35.17	0.067
(target [PFC iTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	-9.95	-28.50 – 8.60	0.293
Random Effects			
σ^2			21098.49
τ_{00} subject			2435.66
ICC			0.10
N subject			24
Observations			22125
Marginal R ² / Conditional R ²			0.058 / 0.156

WORKING MEMORY BIASES ACTIONS

Table 1d. Movement duration

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	418.10	386.96 – 449.25	< 0.001
target [PFC_cTBS]	-9.81	-17.99 – -1.63	0.019
target [PFC iTBS]	-28.38	-36.56 – -20.20	< 0.001
TrialType2	33.01	24.71 – 41.32	< 0.001
BlockType_continuous_centered	-24.48	-48.40 – -0.55	0.045
block_centered	-0.99	-3.21 – 1.24	0.386
target [PFC_cTBS] : TrialType2	8.15	-3.54 – 19.83	0.172
target [PFC iTBS] : TrialType2	11.27	-0.43 – 22.96	0.059
target [PFC_cTBS] * BlockType_continuous_centered	-11.15	-45.01 – 22.71	0.518
target [PFC iTBS] * BlockType_continuous_centered	21.30	-12.70 – 55.30	0.219
TrialType2 * BlockType_continuous_centered	52.87	18.76 – 86.98	0.002
target [PFC_cTBS] * block_centered	2.26	-0.87 – 5.39	0.157
target [PFC iTBS] * block_centered	0.43	-2.67 – 3.53	0.786
TrialType2 * block_centered	3.93	0.77 – 7.08	0.015
BlockType_continuous_centered * block_centered	-2.73	-12.76 – 7.30	0.594
(target [PFC_cTBS] * TrialType2) * BlockType_continuous_centered	14.92	-33.37 – 63.21	0.545
(target [PFC iTBS] * TrialType2) * BlockType_continuous_centered	-19.29	-67.89 – 29.32	0.437
(target [PFC_cTBS] * TrialType2) * block_centered	-2.64	-7.08 – 1.81	0.245
(target [PFC iTBS] * TrialType2) * block_centered	-1.94	-6.38 – 2.49	0.390
(target [PFC_cTBS] * BlockType_continuous_centered) * block_centered	-4.02	-18.13 – 10.09	0.577
(target [PFC iTBS] * BlockType_continuous_centered) * block_centered	3.37	-10.92 – 17.66	0.644
(TrialType2 * BlockType_continuous_centered) * block_centered	7.93	-6.20 – 22.06	0.271
(target [PFC_cTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	-5.39	-25.30 – 14.53	0.596
(target [PFC iTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	-3.72	-24.03 – 16.60	0.720
Random Effects			
σ^2			25297.02
τ_{00} subject			5849.90
ICC			0.19
N subject			24
Observations			22125
Marginal R^2 / Conditional R^2			0.016 / 0.201

WORKING MEMORY BIASES ACTIONS

Table 1e. WM probe accuracy

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.99	0.98 – 0.99	< 0.001
target [PFC_cTBS]	-0.00	-0.01 – 0.01	0.592
target [PFC iTBS]	-0.00	-0.01 – 0.01	0.757
TrialType2	-0.02	-0.03 – -0.01	< 0.001
BlockType_continuous_centered	0.01	-0.01 – 0.03	0.214
block_centered	0.00	-0.00 – 0.00	0.440
target [PFC_cTBS] : TrialType2	0.01	0.00 – 0.02	0.040
target [PFC iTBS] : TrialType2	0.02	0.01 – 0.03	0.003
target [PFC_cTBS] * BlockType_continuous_centered	-0.02	-0.05 – 0.01	0.252
target [PFC iTBS] * BlockType_continuous_centered	-0.03	-0.06 – -0.00	0.042
TrialType2 * BlockType_continuous_centered	-0.01	-0.04 – 0.02	0.441
target [PFC_cTBS] * block_centered	-0.00	-0.00 – 0.00	0.717
target [PFC iTBS] * block_centered	-0.00	-0.00 – 0.00	0.507
TrialType2 * block_centered	0.00	-0.00 – 0.00	0.864
BlockType_continuous_centered * block_centered	-0.00	-0.01 – 0.01	0.961
(target [PFC_cTBS] * TrialType2) * BlockType_continuous_centered	0.02	-0.02 – 0.06	0.398
(target [PFC iTBS] * TrialType2) * BlockType_continuous_centered	0.02	-0.02 – 0.07	0.302
(target [PFC_cTBS] * TrialType2) * block_centered	-0.00	-0.00 – 0.00	0.971
(target [PFC iTBS] * TrialType2) * block_centered	-0.00	-0.00 – 0.00	0.648
(target [PFC_cTBS] * BlockType_continuous_centered) * block_centered	0.00	-0.01 – 0.01	0.769
(target [PFC iTBS] * BlockType_continuous_centered) * block_centered	0.00	-0.01 – 0.01	0.777
(TrialType2 * BlockType_continuous_centered) * block_centered	-0.01	-0.02 – 0.00	0.169
(target [PFC_cTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	0.01	-0.00 – 0.03	0.124
(target [PFC iTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	0.01	-0.01 – 0.02	0.564
Random Effects			
σ^2			0.02
τ_{00} subject			0.00
ICC			0.01
N subject			24
Observations			22125
Marginal R^2 / Conditional R^2			0.003 / 0.012

WORKING MEMORY BIASES ACTIONS

Table 1f. WM probe RT

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	697.65	658.41 – 736.89	< 0.001
target [PFC_cTBS]	-5.43	-17.05 – 6.19	0.359
target [PFC iTBS]	-13.47	-25.10 – -1.85	0.023
TrialType2	18.28	6.49 – 30.08	0.002
BlockType_continuous_centered	-9.11	-43.11 – 24.88	0.599
block_centered	-4.00	-7.16 – -0.84	0.013
target [PFC_cTBS] : TrialType2	-1.95	-18.55 – 14.65	0.818
target [PFC iTBS] : TrialType2	2.09	-14.53 – 18.70	0.806
target [PFC_cTBS] * BlockType_continuous_centered	13.39	-34.72 – 61.50	0.586
target [PFC iTBS] * BlockType_continuous_centered	18.50	-29.80 – 66.81	0.453
TrialType2 * BlockType_continuous_centered	18.48	-29.98 – 66.94	0.455
target [PFC_cTBS] * block_centered	3.02	-1.43 – 7.47	0.184
target [PFC iTBS] * block_centered	1.73	-2.67 – 6.13	0.441
TrialType2 * block_centered	2.92	-1.56 – 7.40	0.202
BlockType_continuous_centered * block_centered	15.55	1.30 – 29.80	0.032
(target [PFC_cTBS] * TrialType2) * BlockType_continuous_centered	-24.06	-92.67 – 44.56	0.492
(target [PFC iTBS] * TrialType2) * BlockType_continuous_centered	-18.83	-87.89 – 50.23	0.593
(target [PFC_cTBS] * TrialType2) * block_centered	-4.94	-11.25 – 1.38	0.125
(target [PFC iTBS] * TrialType2) * block_centered	-4.33	-10.64 – 1.97	0.178
(target [PFC_cTBS] * BlockType_continuous_centered) * block_centered	-19.14	-39.19 – 0.91	0.061
(target [PFC iTBS] * BlockType_continuous_centered) * block_centered	-8.02	-28.32 – 12.28	0.439
(TrialType2 * BlockType_continuous_centered) * block_centered	2.48	-17.61 – 22.56	0.809
(target [PFC_cTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	5.22	-23.07 – 33.51	0.718
(target [PFC iTBS] * TrialType2 * BlockType_continuous_centered) * block_centered	3.94	-24.93 – 32.80	0.789
Random Effects			
σ^2			51071.79
τ_{00} subject			9195.98
ICC			0.15
N _{subject}			24
Observations			22125
Marginal R ² / Conditional R ²			0.003 / 0.155

WORKING MEMORY BIASES ACTIONS

Two-target models (cTBS vs. iTBS)

Table 2a. Movement choice accuracy

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.99	0.99 – 1.00	< 0.001
target [PFC_iTBS]	0.00	-0.00 – 0.01	0.932
TrialType [incompatible]	-0.01	-0.02 – -0.01	< 0.001
BlockType_continuous_centered	0.00	-0.01 – 0.02	0.619
block_centered	-0.00	-0.00 – -0.00	0.041
target [PFC_iTBS] * TrialType [incompatible]	0.00	-0.01 – 0.01	0.732
target [PFC_iTBS] * BlockType_continuous_centered	0.01	-0.01 – 0.03	0.398
TrialType [incompatible] * BlockType_continuous_centered	-0.03	-0.05 – -0.01	0.013
target [PFC_iTBS] * block_centered	0.00	-0.00 – 0.00	0.087
TrialType [incompatible] * block_centered	0.00	0.00 – 0.00	0.006
BlockType_continuous_centered * block_centered	0.00	-0.00 – 0.01	0.442
(target [PFC_iTBS] * TrialType [incompatible]) * BlockType_continuous_centered	0.00	-0.03 – 0.03	0.789
(target [PFC_iTBS] * TrialType [incompatible]) * block_centered	-0.00	-0.01 – -0.00	0.049
(target [PFC_iTBS] * BlockType_continuous_centered) * block_centered	-0.00	-0.01 – 0.01	0.452
(TrialType [incompatible] * BlockType_continuous_centered) * block_centered	0.00	-0.01 – 0.01	0.509
(target [PFC_iTBS] * TrialType [incompatible] * BlockType_continuous_centered) * block_centered	0.00	-0.01 – 0.02	0.545
Random Effects			
σ^2			0.01
τ_{00} subject			0.00
ICC			0.01
N subject			24
Observations			14974
Marginal R^2 / Conditional R^2			0.004 / 0.012

WORKING MEMORY BIASES ACTIONS

Table 2b. Movement trajectory precision

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	10.35	7.39 – 13.31	< 0.001
target [PFC iTBS]	0.21	-1.30 – 1.73	0.781
TrialType [incompatible]	12.25	10.72 – 13.78	< 0.001
BlockType_continuous_centered	-0.92	-5.37 – 3.53	0.685
block_centered	0.30	-0.11 – 0.71	0.150
target [PFC iTBS] * TrialType [incompatible]	-0.68	-2.84 – 1.48	0.538
target [PFC iTBS] * BlockType_continuous_centered	-1.11	-7.43 – 5.22	0.731
TrialType [incompatible] * BlockType_continuous_centered	8.40	2.05 – 14.75	0.010
target [PFC iTBS] * block_centered	-0.10	-0.67 – 0.47	0.735
TrialType [incompatible] * block_centered	0.60	0.02 – 1.18	0.044
BlockType_continuous_centered * block_centered	-1.36	-3.21 – 0.49	0.150
(target [PFC iTBS] * TrialType [incompatible]) * BlockType_continuous_centered	4.56	-4.48 – 13.60	0.323
(target [PFC iTBS] * TrialType [incompatible]) * block_centered	-0.13	-0.95 – 0.69	0.754
(target [PFC iTBS] * BlockType_continuous_centered) * block_centered	0.83	-1.85 – 3.50	0.545
(TrialType [incompatible] * BlockType_continuous_centered) * block_centered	0.13	-2.48 – 2.74	0.922
(target [PFC iTBS] * TrialType [incompatible] * BlockType_continuous_centered) * block_centered	0.81	-2.96 – 4.57	0.674
Random Effects			
σ^2			872.85
τ_{00} subject			47.42
ICC			0.05
N subject			24
Observations			14796
Marginal R^2 / Conditional R^2			0.037 / 0.086

WORKING MEMORY BIASES ACTIONS

Table 2c. Movement initiation

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	487.07	464.51 – 509.63	< 0.001
target [PFC iTBS]	13.81	6.40 – 21.22	< 0.001
TrialType [incompatible]	56.00	48.52 – 63.48	< 0.001
BlockType_continuous_centered	-68.82	-90.62 – -47.03	< 0.001
block_centered	-5.06	-7.06 – -3.05	< 0.001
target [PFC iTBS] * TrialType [incompatible]	-3.55	-14.14 – 7.03	0.511
target [PFC iTBS] * BlockType_continuous_centered	18.75	-12.21 – 49.71	0.235
TrialType [incompatible] * BlockType_continuous_centered	26.49	-4.60 – 57.59	0.095
target [PFC iTBS] * block_centered	3.83	1.03 – 6.63	0.007
TrialType [incompatible] * block_centered	0.28	-2.57 – 3.13	0.846
BlockType_continuous_centered * block_centered	-1.17	-10.23 – 7.89	0.801
(target [PFC iTBS] * TrialType [incompatible]) * BlockType_continuous_centered	-9.85	-54.11 – 34.40	0.663
(target [PFC iTBS] * TrialType [incompatible]) * block_centered	-2.94	-6.97 – 1.08	0.152
(target [PFC iTBS] * BlockType_continuous_centered) * block_centered	13.61	0.50 – 26.71	0.042
(TrialType [incompatible] * BlockType_continuous_centered) * block_centered	14.77	2.00 – 27.54	0.023
(target [PFC iTBS] * TrialType [incompatible] * BlockType_continuous_centered) * block_centered	-26.39	-44.83 – -7.95	0.005
Random Effects			
σ^2			20920.12
τ_{00} subject			3007.24
ICC			0.13
N subject			24
Observations			14796
Marginal R ² / Conditional R ²			0.053 / 0.172

WORKING MEMORY BIASES ACTIONS

Table 2d. Movement duration

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	408.25	375.17 – 441.32	<0.001
target [PFC_iTBS]	-18.58	-26.70 – -10.47	<0.001
TrialType [incompatible]	41.31	33.12 – 49.50	<0.001
BlockType_continuous_centered	-34.48	-58.35 – -10.61	0.005
block_centered	1.32	-0.88 – 3.51	0.239
target [PFC_iTBS] * TrialType [incompatible]	2.62	-8.97 – 14.21	0.658
target [PFC_iTBS] * BlockType_continuous_centered	32.09	-1.83 – 66.00	0.064
TrialType [incompatible] * BlockType_continuous_centered	67.12	33.06 – 101.17	<0.001
target [PFC_iTBS] * block_centered	-1.97	-5.04 – 1.10	0.209
TrialType [incompatible] * block_centered	1.28	-1.84 – 4.41	0.420
BlockType_continuous_centered * block_centered	-8.13	-18.05 – 1.80	0.108
(target [PFC_iTBS] * TrialType [incompatible]) * BlockType_continuous_centered	-33.12	-81.59 – 15.36	0.181
(target [PFC_iTBS] * TrialType [incompatible]) * block_centered	0.63	-3.78 – 5.03	0.781
(target [PFC_iTBS] * BlockType_continuous_centered) * block_centered	8.33	-6.03 – 22.69	0.255
(TrialType [incompatible] * BlockType_continuous_centered) * block_centered	2.83	-11.16 – 16.81	0.692
(target [PFC_iTBS] * TrialType [incompatible] * BlockType_continuous_centered) * block_centered	-1.28	-21.48 – 18.92	0.901
Random Effects			
σ^2			25097.70
τ_{00} subject			6630.64
ICC			0.21
N subject			24
Observations			14796
Marginal R ² / Conditional R ²			0.017 / 0.222

WORKING MEMORY BIASES ACTIONS

Table 2e. WM probe accuracy

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.98	0.98 – 0.99	< 0.001
target [PFC iTBS]	0.00	-0.01 – 0.01	0.815
TrialType [incompatible]	-0.01	-0.01 – -0.00	0.045
BlockType_continuous_centered	-0.00	-0.02 – -0.02	0.713
block_centered	0.00	-0.00 – -0.00	0.766
target [PFC iTBS] * TrialType [incompatible]	0.00	-0.01 – -0.01	0.336
target [PFC iTBS] * BlockType_continuous_centered	-0.01	-0.04 – -0.02	0.346
TrialType [incompatible] * BlockType_continuous_centered	0.01	-0.02 – -0.04	0.671
target [PFC iTBS] * block_centered	-0.00	-0.00 – -0.00	0.744
TrialType [incompatible] * block_centered	0.00	-0.00 – -0.00	0.903
BlockType_continuous_centered * block_centered	0.00	-0.01 – -0.01	0.800
(target [PFC iTBS] * TrialType [incompatible]) * BlockType_continuous_centered	0.00	-0.04 – -0.05	0.833
(target [PFC iTBS] * TrialType [incompatible]) * block_centered	-0.00	-0.00 – -0.00	0.663
(target [PFC iTBS] * BlockType_continuous_centered) * block_centered	0.00	-0.01 – -0.01	0.934
(TrialType [incompatible] * BlockType_continuous_centered) * block_centered	0.01	-0.01 – -0.02	0.373
(target [PFC iTBS] * TrialType [incompatible] * BlockType_continuous_centered) * block_centered	-0.01	-0.03 – -0.01	0.309
Random Effects			
σ^2			0.02
τ_{00} subject			0.00
ICC			0.01
N subject			24
Observations			14796
Marginal R^2 / Conditional R^2			0.001 / 0.009

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Table 2f. WM probe RT

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	692.31	648.68 – 735.95	<0.001
target [PFC_iTBS]	-8.10	-19.67 – 3.47	0.170
TrialType [incompatible]	16.59	4.92 – 28.27	0.005
BlockType_continuous_centered	4.66	-29.38 – 38.70	0.788
block_centered	-1.02	-4.15 – 2.11	0.521
target [PFC_iTBS] * TrialType [incompatible]	3.49	-13.04 – 20.02	0.679
target [PFC_iTBS] * BlockType_continuous_centered	5.53	-42.82 – 53.89	0.823
TrialType [incompatible] * BlockType_continuous_centered	-5.90	-54.46 – 42.66	0.812
target [PFC_iTBS] * block_centered	-1.31	-5.68 – 3.07	0.559
TrialType [incompatible] * block_centered	-1.85	-6.30 – 2.61	0.417
BlockType_continuous_centered * block_centered	-3.03	-17.18 – 11.12	0.675
(target [PFC_iTBS] * TrialType [incompatible]) * BlockType_continuous_centered	5.00	-64.12 – 74.12	0.887
(target [PFC_iTBS] * TrialType [incompatible]) * block_centered	0.58	-5.70 – 6.86	0.856
(target [PFC_iTBS] * BlockType_continuous_centered) * block_centered	9.76	-10.71 – 30.23	0.350
(TrialType [incompatible] * BlockType_continuous_centered) * block_centered	7.58	-12.36 – 27.52	0.456
(target [PFC_iTBS] * TrialType [incompatible] * BlockType_continuous_centered) * block_centered	-1.19	-29.99 – 27.61	0.935
Random Effects			
σ^2			51028.95
τ_{00} subject			11478.95
ICC			0.18
N subject			24
Observations			14796
Marginal R ² / Conditional R ²			0.003 / 0.186

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Trial history models (current x previous trial compatibility)

Table 3a. Movement choice accuracy

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.99	0.99 – 1.00	< 0.001
TrialType [incompatible]	-0.02	-0.03 – -0.00	0.011
prev_trial_type [incompatible]	-0.00	-0.02 – 0.01	0.454
target [PFC_cTBS]	0.00	-0.01 – 0.02	0.585
target [PFC iTBS]	-0.00	-0.01 – 0.01	0.778
TrialType [incompatible] * prev_trial_type [incompatible]	0.01	-0.00 – 0.03	0.132
TrialType [incompatible] * target [PFC_cTBS]	-0.00	-0.02 – 0.02	0.846
TrialType [incompatible] * target [PFC iTBS]	0.01	-0.01 – 0.02	0.428
prev_trial_type [incompatible] * target [PFC_cTBS]	0.00	-0.02 – 0.02	0.992
prev_trial_type [incompatible] * target [PFC iTBS]	0.00	-0.02 – 0.02	0.793
(TrialType [incompatible] * prev_trial_type [incompatible]) * target [PFC_cTBS]	-0.01	-0.04 – 0.01	0.361
(TrialType [incompatible] * prev_trial_type [incompatible]) * target [PFC iTBS]	-0.01	-0.04 – 0.01	0.321
Random Effects			
σ^2			0.01
τ_{00} subject			0.00
ICC			0.01
N subject			24
Observations			7233
Marginal R ² / Conditional R ²			0.004 / 0.010

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Table 3b. Movement trajectory precision

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	10.66	6.68 – 14.64	<0.001
TrialType [incompatible]	9.76	6.35 – 13.16	<0.001
prev_trial_type [incompatible]	1.61	-1.77 – 5.00	0.350
target [PFC_cTBS]	0.04	-3.35 – 3.44	0.980
target [PFC_iTBS]	-1.31	-4.75 – 2.12	0.454
TrialType [incompatible] * prev_trial_type [incompatible]	-2.49	-7.32 – 2.35	0.314
TrialType [incompatible] * target [PFC_cTBS]	1.47	-3.32 – 6.26	0.548
TrialType [incompatible] * target [PFC_iTBS]	2.40	-2.41 – 7.21	0.329
prev_trial_type [incompatible] * target [PFC_cTBS]	-1.56	-6.31 – 3.19	0.521
prev_trial_type [incompatible] * target [PFC_iTBS]	-0.15	-4.92 – 4.62	0.950
(TrialType [incompatible] * prev_trial_type [incompatible]) * target [PFC_cTBS]	1.77	-5.04 – 8.57	0.611
(TrialType [incompatible] * prev_trial_type [incompatible]) * target [PFC_iTBS]	-1.87	-8.69 – 4.94	0.590
Random Effects			
σ^2			889.65
τ_{00} subject			62.03
ICC			0.07
N subject			24
Observations			7137
Marginal R^2 / Conditional R^2			0.026 / 0.089

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Table 3c. Movement initiation

<i>3-target Model Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	478.48	457.03 – 499.94	< 0.001
TrialType [incompatible]	76.88	60.84 – 92.92	< 0.001
prev_trial_type [incompatible]	30.31	14.38 – 46.24	< 0.001
target [PFC_cTBS]	3.75	-12.23 – 19.73	0.645
target [PFC_iTBS]	11.71	-4.47 – 27.89	0.156
TrialType [incompatible] * prev_trial_type [incompatible]	-41.63	-64.41 – -18.84	< 0.001
TrialType [incompatible] * target [PFC_cTBS]	-17.04	-39.61 – 5.53	0.139
TrialType [incompatible] * target [PFC_iTBS]	-1.15	-23.81 – 21.51	0.921
prev_trial_type [incompatible] * target [PFC_cTBS]	-13.32	-35.70 – 9.05	0.243
prev_trial_type [incompatible] * target [PFC_iTBS]	-1.70	-24.17 – 20.78	0.882
(TrialType [incompatible] * prev_trial_type [incompatible]) * target [PFC_cTBS]	43.70	11.66 – 75.75	0.008
(TrialType [incompatible] * prev_trial_type [incompatible]) * target [PFC_iTBS]	5.70	-26.39 – 37.79	0.728
Random Effects			
σ^2			19733.66
τ_{00} subject			2057.54
ICC			0.09
N _{subject}			24
Observations			7137
Marginal R ² / Conditional R ²			0.043 / 0.133
<i>2-target Model Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	482.68	459.64 – 505.72	< 0.001
TrialType [incompatible]	59.14	43.19 – 75.09	< 0.001
prev_trial_type [incompatible]	16.32	0.54 – 32.10	0.043
target2	7.62	-8.41 – 23.66	0.352
TrialType [incompatible] * prev_trial_type [incompatible]	3.55	-19.09 – 26.20	0.758
TrialType [incompatible] : target2	16.35	-6.30 – 39.01	0.157
prev_trial_type [incompatible] : target2	12.27	-10.15 – 34.69	0.283
TrialType [incompatible] : prev_trial_type [incompatible] : target2	-39.26	-71.34 – -7.18	0.016
Random Effects			
σ^2			19903.52
τ_{00} subject			2532.53
ICC			0.11
N _{subject}			24
Observations			4789
Marginal R ² / Conditional R ²			0.043 / 0.151

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Table 3d. Movement duration

<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	404.21	371.34 – 437.08	<0.001
TrialType [incompatible]	42.53	24.14 – 60.91	<0.001
prev_trial_type [incompatible]	15.41	-2.86 – 33.67	0.098
target [PFC_cTBS]	8.22	-10.10 – 26.54	0.379
target [PFC_iTBS]	-17.20	-35.75 – 1.34	0.069
TrialType [incompatible] * prev_trial_type [incompatible]	-25.00	-51.12 – 1.12	0.061
TrialType [incompatible] * target [PFC_cTBS]	5.95	-19.93 – 31.82	0.652
TrialType [incompatible] * target [PFC_iTBS]	6.81	-19.16 – 32.78	0.607
prev_trial_type [incompatible] * target [PFC_cTBS]	-6.79	-32.44 – 18.86	0.604
prev_trial_type [incompatible] * target [PFC_iTBS]	-6.83	-32.59 – 18.93	0.603
(TrialType [incompatible] * prev_trial_type [incompatible]) * target [PFC_cTBS]	-5.74	-42.48 – 30.99	0.759
(TrialType [incompatible] * prev_trial_type [incompatible]) * target [PFC_iTBS]	10.08	-26.70 – 46.87	0.591
Random Effects			
σ^2			25930.95
τ_{00} subject			5673.64
ICC			0.18
N subject			24
Observations			7137
Marginal R^2 / Conditional R^2			0.013 / 0.191

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