Cognitive capacity limits are remediated by practice-induced plasticity in a striatal-cortical network

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Analysis code: https://github.com/kel-github/multi-practice-repository

Raw data: https://espace.library.uq.edu.au/view/UQ:370251

Processed data: To access the processed data please email getkellygarner@gmail.com

Abstract

Humans show striking limitations in information processing when multitasking, yet can modify these limits with practice. Such limitations have been attributed to the capacity of a frontal-parietal network, but recent models of decision-making implicate a striatal-cortical network. We adjudicated these accounts by implementing a dynamic causal modelling (DCM) analysis of a functional magnetic resonance imaging (fMRI) dataset, where 100 participants completed a multitasking paradigm in the scanner, before and after engaging in a multitasking (N=50) or an active control (N=50) practice regimen. We observed that multitasking costs, and their practice related remediation, are best explained by modulations in information transfer between the striatum and the cortical areas that represent stimulus-response mappings. Neither multitasking nor practice modulated direct frontal-parietal connectivity. Our results support the view that limits in cognitive capacity are striatally driven, and moderated by the interplay of information exchange from the putamen to the pre-supplementary motor area.

Although human information processing is fundamentally limited, the points at which task difficulty or complexity incurs performance costs are malleable with practice. For example, practicing component tasks reduces the response slowing that is typically induced as a consequence of attempting to complete the same tasks concurrently (multitasking) (Telford 1931; Ruthruff, Johnston, and Van Selst 2001; Strobach and Torsten 2017). These limitations are currently attributed to competition for representation in a frontal-parietal network (Watanabe and Funahashi 2014, 2018; Garner and Dux 2015; Marti, King, and Dehaene 2015), in which the constituent neurons are assumed to adapt response properties in order to represent the contents of the current cognitive episode (Duncan 2010, 2013; Woolgar et al. 2011). Despite recent advances, our understanding of the network dynamics that drive multitasking costs and the influence of practice remains unknown. Furthermore, although recent work has focused on understanding cortical contributions to multitasking limitations, multiple theoretical models implicate striatal-cortical circuits as important neurophysiological substrates for the performance of single sensorimotor decisions (Caballero, Humphries, and Gurney 2018; Bornstein and Daw 2011; Joel, Niv, and Ruppin 2002), the formation of stimulus-response representations in frontal-parietal cortex (Hélie, Ell, and Ashby 2015; Ashby, Turner, and Horvitz 2010), and performance of both effortful and habitual sensorimotor tasks (Yin and Knowlton 2006; Graybiel and Grafton 2015; Jahanshahi et al. 2015). This suggests that a complete account of cognitive limitations and their practice-induced attenuation also requires interrogation into the contribution of striatal-cortical circuits. We seek to address these gaps in understanding by investigating how multitasking and practice influence network dynamics between striatal and cortical regions previously implicated in the cognitive limitations that give rise to multitasking costs (Garner and Dux 2015).

We previously observed that improvements in the decodability of component tasks in two regions of the frontal-parietal network - pre-supplementary motor area (pre-SMA/SMA), the intraparietal sulcus (IPS) - and one region of the striatum (putamen) predicted practice-induced multitasking improvements (Garner and Dux 2015). This implies that practice may not divert performance from the frontal-parietal system, as had been previously assumed (Chein and Schneider 2012; Yin and Knowlton 2006; Kelly and Garavan 2005; Petersen et al. 1998), but rather, may alleviate multitasking costs by reducing competition for representation within the same system. Moreover, our finding that the putamen showed changes to task decodability that predicted behavioural improvements comparable to what was observed for pre-SMA and IPS implies that rather than stemming from overload of an entirely cortical network (Dux et al. 2006; Marti, King, and Dehaene 2015; Marois and Ivanoff 2005), multitasking costs are manifest by limitations within a distributed striatal-cortical system. This raises the question of how interactions between these brain regions give rise to multitasking costs and how can these be mitigated with practice: Do multitasking costs reflect over-taxation of striatal-cortical circuits? Or are they a consequence of competition for representation between cortical areas? Alternately, do multitasking costs stem from limitations in both striatal-cortical and corticocortical connections? Does practice alleviate multitasking costs via modulating all the interregional couplings that give rise to multitasking behaviour, or by selectively increasing or reducing couplings between specific regions?

Our aim was to arbitrate between these possibilities by applying dynamic causal modelling (DCM, Friston, Harrison, and Penny 2003) to an fMRI dataset (N=100) collected while participants performed a

multitasking paradigm before and after practice on the same paradigm (N=50) or on an active control task (N=50) (Garner and Dux 2015). We sought to first characterise the modulatory influence of multitasking on the network dynamics between the pre-SMA, IPS and putamen, and then to understand how practice modulated these network dynamics to drive multitasking performance improvements.

Results

As all results unrelated to the dynamic causal modelling analysis are described in detail in Garner and Dux (2015), we recap the relevant findings here. Participants completed a multitasking paradigm (Figure 1a) while being scanned with functional magnetic resonance imaging (fMRI), in a slow event-related design. For the multitasking paradigm, participants completed both single- and multi-task trials. For the single-task trials, participants made a 2-alternative discrimination between either one of two equiprobable shapes (visual-manual task), or between one of two equiprobable sounds (auditory-manual task). Participants were instructed to make the correct button-press as quickly and as accurately as possible. On multitask trials, the shape and sound stimuli were presented simultaneously, and participants were required to make both discriminations (visual-manual task and auditory-manual task) as quickly and as accurately as possible. Between the pre- and post-practice scanning sessions, participants were randomly allocated to a practice group or an active-control group (also referred to as the control group). The practice group performed the multitask paradigm over multiple days whereas the control group practiced a visual-search task (Figure 1b). For both groups, participants were adaptively rewarded for maintaining accuracy while reducing response-time (see methods section for details).

Our key behavioural measure of multitasking costs was the difference in response-time (RT) between the single- and multi-task conditions. Performing the component tasks as a multitask increases RT for both tasks, relative to when each is performed alone as a single task. The effectiveness of the paradigm to assess multitasking was confirmed with multitasking costs being clearly observed in the pre-practice session (main effect of condition, single- vs multi-task, $F(1, 98) = 688.74$, $MSE = .026$, $p<.0001$, $\eta_p^2 = .88$, see extended Figure 1a). Critically, the practice group showed a larger reduction in multitasking costs between the pre- and post- practice sessions than the control group (significant session (pre vs. post) x condition (single-task vs multitask) x group (practice vs control) interaction; $F(1, 98) = 31.12$, $MSE = .01$, $p < .001$, $\eta_p^2 = .24$, Figure 1c). Specifically, the practice group showed a mean reduction (pre-cost - post-cost) of 293 ms (95% CI [228, 358]) whereas the control group showed a mean reduction of 79 ms (95% CI: [47, 112]). These findings did not appear to be due to a speed/accuracy trade-off as the group x session x condition interaction performed on the accuracy data was not statistically significant ($p=.06$).

We sought to identify the brain regions that could be part of the network that 1) showed increased activity for both single tasks, as could be expected by brain areas containing neurons that adapt to represent the current cognitive episode, 2) showed sensitivity to multitasking demands (i.e. increased activity for multitask relative to single-task trials), and 3) showed specificity in response to the training regimen, i.e. showed a group x session interaction (see Garner and Dux 2015 for details). This criteria isolated the pre-SMA/SMA, the left and right inferior parietal sulcus (IPS) and the left and right putamen. For the current study, in the interest of parsimony over the number of areas (nodes) in our models, and

given we had no strong reason to assume lateralized differences in the function of the underlying network, we opted to include only the pre-SMA/SMA and the remaining left hemisphere regions as our ROIs (Figure 1d).

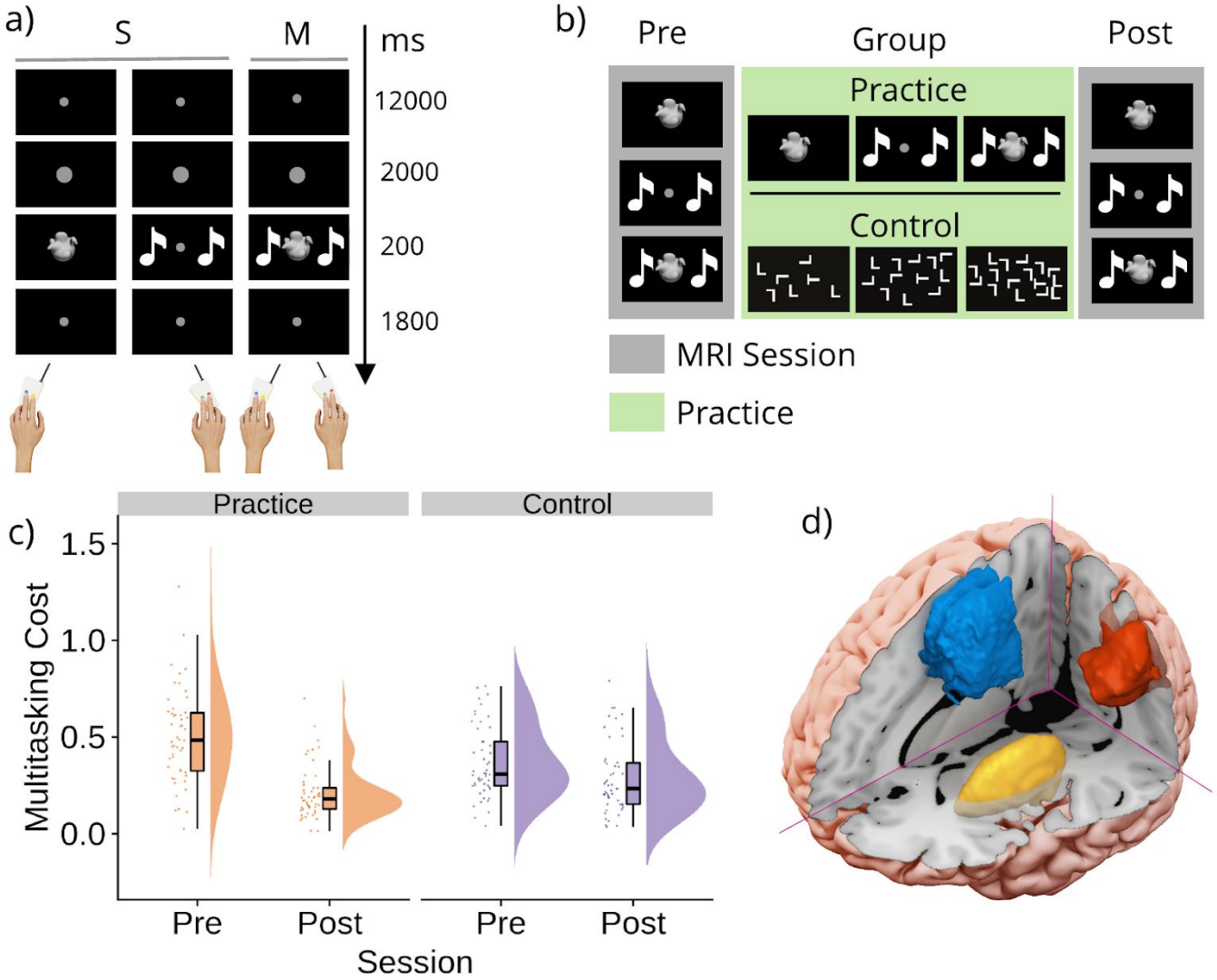
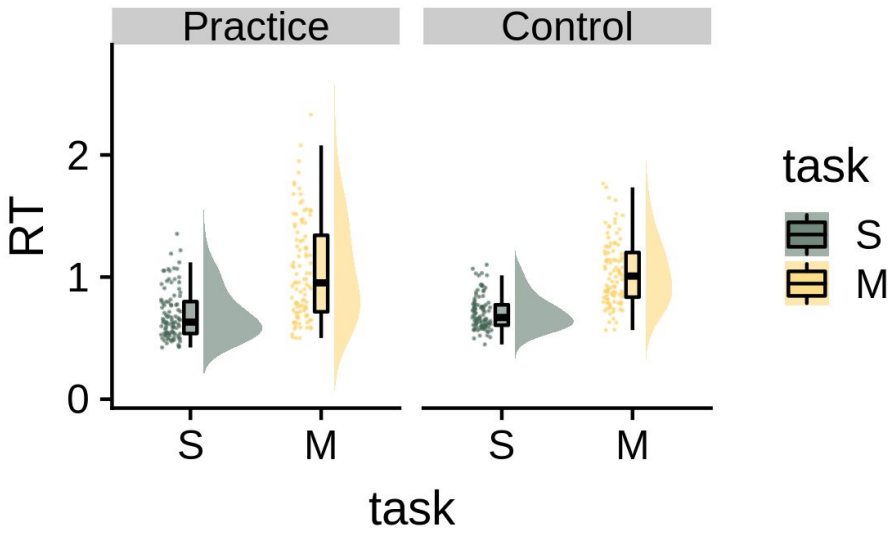


Figure 1: Task, protocol, behaviour and regions of interest. a) Multitasking paradigm: The task was comprised of two single-task (S) conditions and one multitask (M) condition. Each S was a 2 alternative-discrimination between either one of two equiprobable stimuli. The stimuli could either be shapes (visual-manual task), or sounds (auditory-manual task). On M trials, participants were required to complete both Ss (visual-manual and auditory-manual). On all trials, participants were requested to perform the task(s) as quickly and as accurately as possible. b) Protocol: At both the pre- and post- practice sessions, all participants completed the multitasking paradigm while structural and functional MRI images were taken. Participants were then allocated to either the practice or the active-control group. The practice group subsequently performed the multitask paradigm over three sessions, whereas the control group practiced a visual-search task with three levels of difficulty, under a comparable reinforcement regimen. c) Multitasking costs to response time [mean(Ms) - mean(Ss)] for the practice and control groups, at the pre- and post-practice sessions, presented as individual data points, boxplots and densities. d) Regions of interest identified by our previous study (Garner and Dux, 2015); the Supplementary Motor Area (blue), the Intraparietal Sulcus (red), and the Putamen (yellow).



Extended Figure 1a: Dot, box and density plots for mean response-times (RT) for the single- (S) and multitasks (M) for the practice and the control groups at the pre-training session.

Network dynamics underlying multitasking

We sought to identify how multitasking modulates connectivity between the IPS, pre-SMA/SMA and the putamen (although our anatomically defined mask included all of SMA, 78% of participants showed peak activity in pre-SMA, defined as coordinates rostral to the vertical commissure anterior (Kim et al. 2010), so we hereon refer to the region as pre-SMA, note: the within group percentages were also comparable; practice = 83 %, control = 73 %). To achieve this, we first applied DCM to construct hypothetical networks that could underlie the observed data. These models were then grouped into families on the basis of characteristics that addressed our key questions. This allowed us to conduct random effects family-level inference (Penny et al. 2010) to determine which model characteristics were most likely, given the data. Specifically we asked; 1) which region drives inputs to the multitasking network (putamen or IPS family, Figure 2a)? and 2) does multitasking modulate striatal-cortical couplings, corticocortical couplings or both (Figure 2b)? Lastly, we conducted Bayesian Model Averaging (BMA) within the winning family to make inference over which specific parameters were modulated by multitasking (i.e. is the posterior estimate for each connection reliably different from 0?).

The model space (Extended Figure 2a) which underpins our theoretically motivated hypothetical networks contained bidirectional endogenous connections between all three regions, owing to evidence for the existence of anatomical connections between the putamen, IPS and pre-SMA (Cavada and Goldman-Rakic 1989; Luppino et al. 1993; Haber 2016; Alexander, DeLong, and Strick 1986; Wise et al. 1997), as well as endogenous self-connections. As we had no a priori reason to exclude a modulatory influence of multitasking on any specific direction of coupling, we considered all 63 possible combinations of modulation (see extended Figure 2b).

First we asked which region in the network received driving inputs that are modulated by multitasking demands. As the IPS shows sensitivity to sensory inputs across modalities (Vossel, Geng, and Fink 2014; Anderson et al. 2010; Grefkes and Fink 2005), and as the striatum receives sensory-inputs from both the thalamus (Alloway et al. 2017) and from sensory cortices (Saint-Cyr, Ungerleider, and Desimone

1990; Guo et al. 2018; Reig and Silberberg 2014), both IPS and putamen were considered as possible candidates. We therefore fit each of the 63 modulatory models twice, once allowing driving inputs to occur via the IPS, and once allowing input via the putamen (therefore, total models [M_i] = 126). These models were grouped into two families, on the basis of their input (*IPS input* family [f_{IPS}] and *putamen input* family [f_{Put}]). The evidence favoured the *putamen* family (expected probability [$p(f_{Put}|Y)$]: .54, exceedance probability ($p(f_{Put}|Y > f_{IPS}|Y)$: .79, Figure 2a) relative to the *IPS* family. Therefore, the data are best explained by models where multitasking modulates driving inputs to the putamen. The winning *putamen input* family were retained for the next stage of family level comparisons.

We then asked whether the data were better explained by models that allowed multitasking to modulate *striatal-cortical* connections, *corticocortical* connections or *all* (Figure 2b). We therefore grouped the models from the putamen input family into three groups. The *striatal-cortical family* [f_{SC}] contained models that allowed multitasking to modulate any combination of the striatal-cortical connections, and none of the corticocortical connections. The *corticocortical family* [f_{CC}] contained models with the opposite pattern; multitasking could modulate any pattern of corticocortical couplings and none of the striatal-cortical couplings). Finally, in the *all family*, we considered models that included modulations to both striatal-cortical and corticocortical couplings [f_{ALL}]). In support of the idea that multitasking modulates striatal-cortical connectivity as well as corticocortical connections, the evidence favoured the *all* family ($p(f_{ALL}|Y)$: .86, $p(f_{ALL}|Y > f_{SC,\ CC}|Y) = 1$) over the *striatal-cortical* family ($p(f_{SC}|Y)$: .11) and the *corticocortical* family ($p(f_{CC}|Y)$: .03).

Having determined that multitasking is indeed supported by both striatal-cortical and corticocortical couplings, we next sought to infer which specific parameters were modulated by multitasking; i.e. do we have evidence for bidirectional endogenous couplings between all regions? Or a subset of endogenous couplings? With regard to multitasking related modulations; are all couplings modulated, or a subset of striatal-cortical and corticocortical connections? To answer this we conducted BMA over the *all* family to obtain the posteriors over each of the endogenous (A) and modulatory coupling (B) parameters. We looked for A parameters to retain by testing for which posteriors showed a probability of difference (Pp) from zero that was greater than .99 (applying the Sidak adjustment for multiple comparisons). As seen in the extended Figure 2c, we retain endogenous couplings from IPS to Put, Put to IPS, Put to pre-SMA, and pre-SMA to IPS (all Pps = 1) and reject endogenous couplings from IPS to pre-SMA (Pp = .98) and pre-SMA to Put (Pp = .66). We applied the same test to the B parameters and found evidence for a modulatory influence of multitasking on Put to IPS coupling (Pp = 1). We reject a modulatory influence of multitasking on the remaining parameters (all Pps <= .98), although we are more tentative with conclusions regarding Put to pre-SMA coupling, as this is the only one of the rejected set that showed reasonably strong evidence for a modulatory influence (Pp = .96), with posterior distributional characteristics that were similar to that for the retained modulatory parameter (i.e. a smaller standard deviation that was closer to that observed for Put to IPS coupling (σ = .06 for both), than for the rejected couplings (all σ > .08)), and with strong evidence for the corresponding endogenous parameter (Pp = 1, Figure 2c). It is interesting, that neither the probability of modulation to the pre-SMA to IPS (Pp = .82) nor the IPS to pre-SMA parameters (Pp = .88) survived correction for inclusion in the model, even though there was strong evidence for an

endogenous connection between pre-SMA and IPS, and given that f_{ALL} was the preferred family. It is possible that while these connections are modulated, the strength of modulations varies more across individuals that for the connections for which strong evidence was obtained.

To sum up (Figure 2d), the influence of multitasking is best explained by a network where information is propagated, via Put, to the IPS and the pre-SMA. Information is shared back to the Put via IPS, and from pre-SMA to IPS. Multitasking demands specifically increases the rate of information transfer sent from the Put to IPS, and possibly from Put to pre-SMA. Hence, we can reject the idea that multitasking costs are solely due to limitations in a cortical network, and rather reflect the taxation of information sharing between the Put and the other relevant cortical areas, namely the IPS and the pre-SMAs.

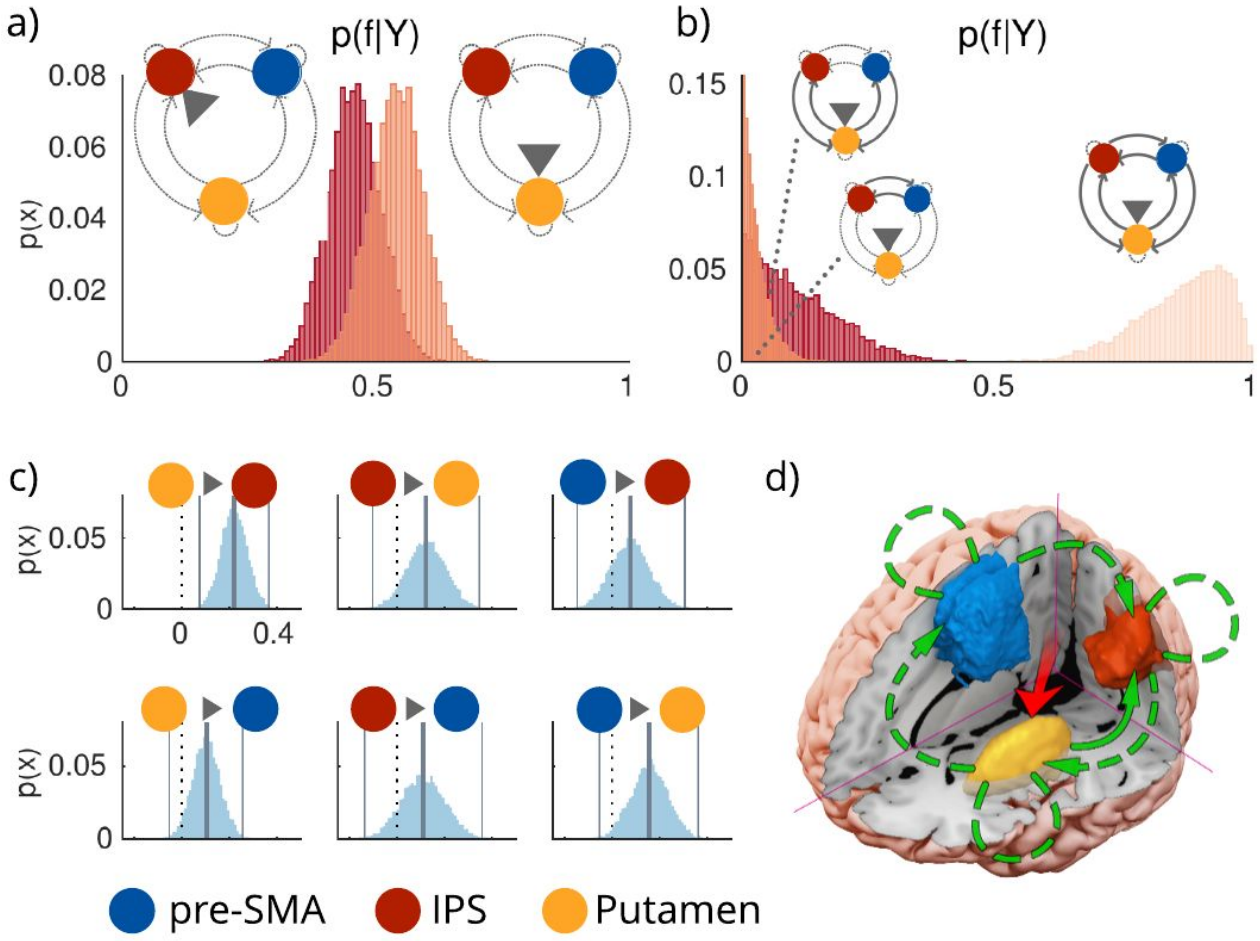
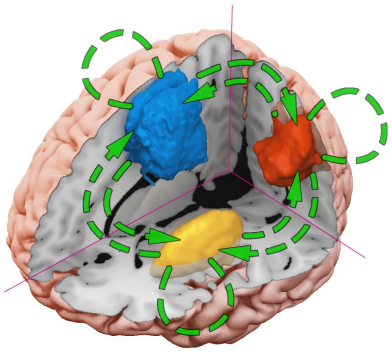
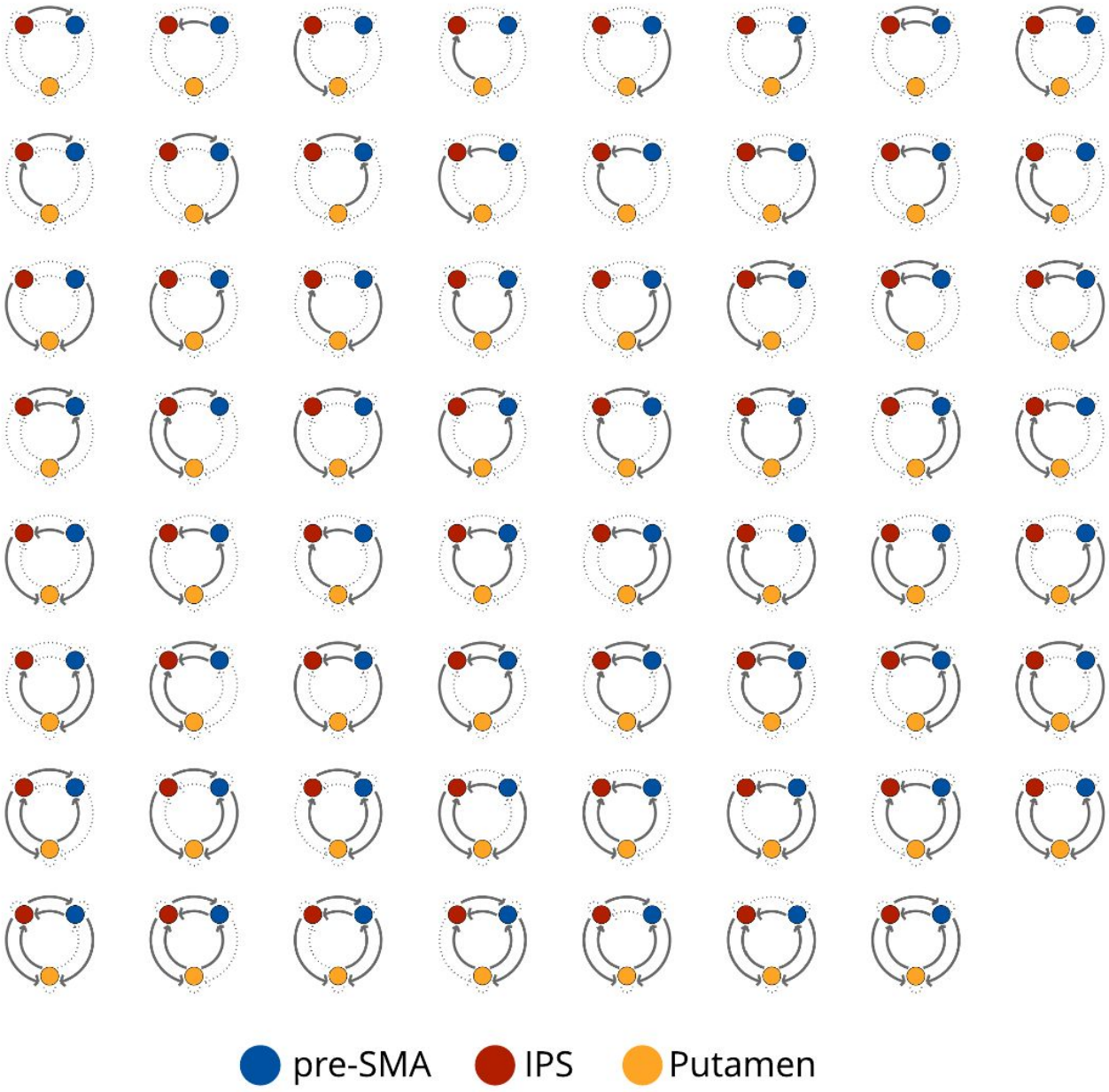


Figure 2: The modulatory influence of multitasking on the pre-SMA/IPS/Putamen network. a) Posterior probabilities over families, given the data [p(f|Y)], defined by inputs to IPS (left distribution) or Putamen (right distribution). The evidence favours driving inputs via Putamen. b) Posterior probabilities over families differing in the connections modulated by multitasking (from left to right: corticostriatal modulations, corticocortical modulations, or both). Model evidence favours both corticostriatal and corticocortical couplings. c) Posterior distributions over B parameters. Vertical lines reflect posterior means and 99th percentiles, whereas the dotted black line = 0. Multitasking reliably increased modulatory coupling from the putamen to the IPS. To view the posterior distributions that informed the removal of endogenous model connections, please check extended figure 2c. d) Proposed model for the modulatory influence of multitasking (see extended Figure 2b, for the posteriors distributions over the A parameters that motivate removal of IPS to pre-SMA and pre-SMA to Putamen). p(x) = probability of sample from posterior density. Connections drawn with a continuous line denote significantly modulated (by multitasking) connections

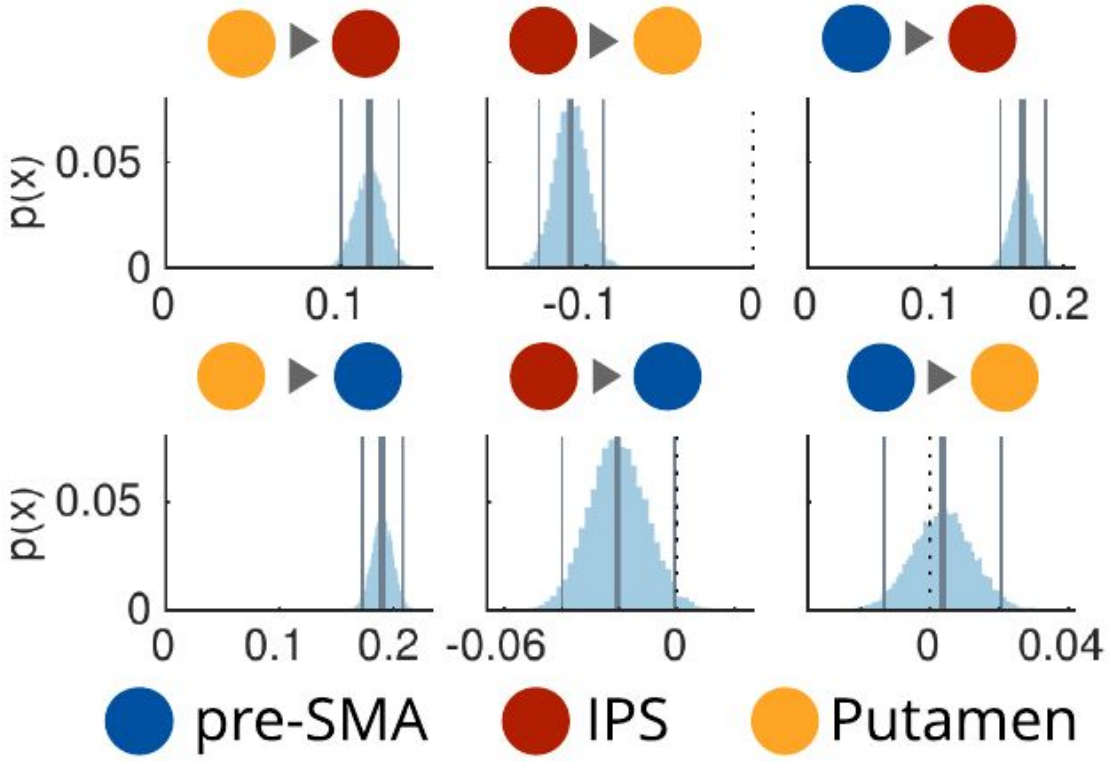
(according to DCM.B in 2c) whereas dashed lines represent the functionally present connections (according to DCM.A in Extended Figure 2b).



Extended Figure 2a: The anatomical model contained bidirectional endogenous connections between all three regions, as well as endogenous self-connections.



Extended Figure 2b: We modelled all 63 possible modulatory influences of multitasking. Dotted lines = endogenous connections, solid lines = modulatory connections. Each pair of regions contains bidirectional coupling.



Extended Figure 2c: Posterior probabilities over A parameters. p(x) = probability of sample from posterior density.

The influence of practice on the network underpinning multitasking

Next we sought to understand how practice influences the network that underpins multitasking on both single- and multi-task trials, for both the practice and control groups. For example, it may be that practice influences all the endogenous couplings in the network, or a subset of them. Furthermore, if practice only modulated a subset of couplings, would it only be on striatal-cortical couplings, or corticocortical, or both? By comparing the practice group to the control group, we sought to identify which modulations are due to engagement with a multitasking regimen, and which are due to repeating the task at the post-session (and potentially due to engagement with a practice regimen that did not include multitasking). To address these questions, we constructed DCMs that allowed practice (i.e. a pre/post session factor) to modulate all the possible combinations of couplings in the multitasking network defined above (4 possible connections, therefore M_i = 15, see extended Figure 3a). We then fit these DCMs separately to the single-task data and to the multitask data, concatenated across pre- to post- sessions. Comparable to above, we decided to leverage information across models (proportional to the probability of the model, see extended Figure 3b) and conducted random-effects BMA across the model space to estimate posteriors over the parameters. This method can be more robust when the model space includes larger numbers of models that share characteristics, as it helps overcome dependence on the comparison set by identifying the likely features that are common across models (Penny et al. 2010). We compare the

resulting posteriors over parameters to determine for each group, those which deviate reliably from zero for single-task trials, for multitask trials, and also whether they differ between groups (applying the Sidak correction for each set of comparisons).

The results from the analysis of posteriors over parameters can be seen in Figure 3. All practice related modulations influenced striatal-cortical couplings. For single-task trials, in the practice group, the practice factor modulated coupling from IPS to Put (Pp = .99), which was also larger than that observed for the control group (Pp practice > control = .99). No other modulatory couplings achieved the criteria for significance (all Pps <= .96). For the control group, the practice factor modulated both Put to IPS (Pp = .97) and Put to pre-SMA (Pp = 1) couplings. In both cases, the modulatory influence of practice on this coupling was larger for the control group than for the practice group (Pps control > practice = .99, 1). The remaining coupling parameters did not achieve statistical significance (Pps < .8). Thus practice on single-task trials specifically modulates couplings from cortex (IPS to striatum), whereas repeating a task at the post-session (control group) modulates couplings projecting from striatum to cortex. For multitask trials, both groups showed practice related increases to modulations of the putamen to pre-SMA coupling (practice group Pp = .99, control Pp = 1). Perhaps counterintuitively, these were larger for the control group than for the practice group (Pp control > practice = 1), although we dissect this relationship further in the analysis below. The remaining modulatory parameters and group differences did not achieve statistical significance (all Pps <= .93). Therefore, changes from putamen to pre-SMA connections underpin reductions in multitasking costs. Interestingly, practice does not modulate corticocortical activity to improve multitasking performance.

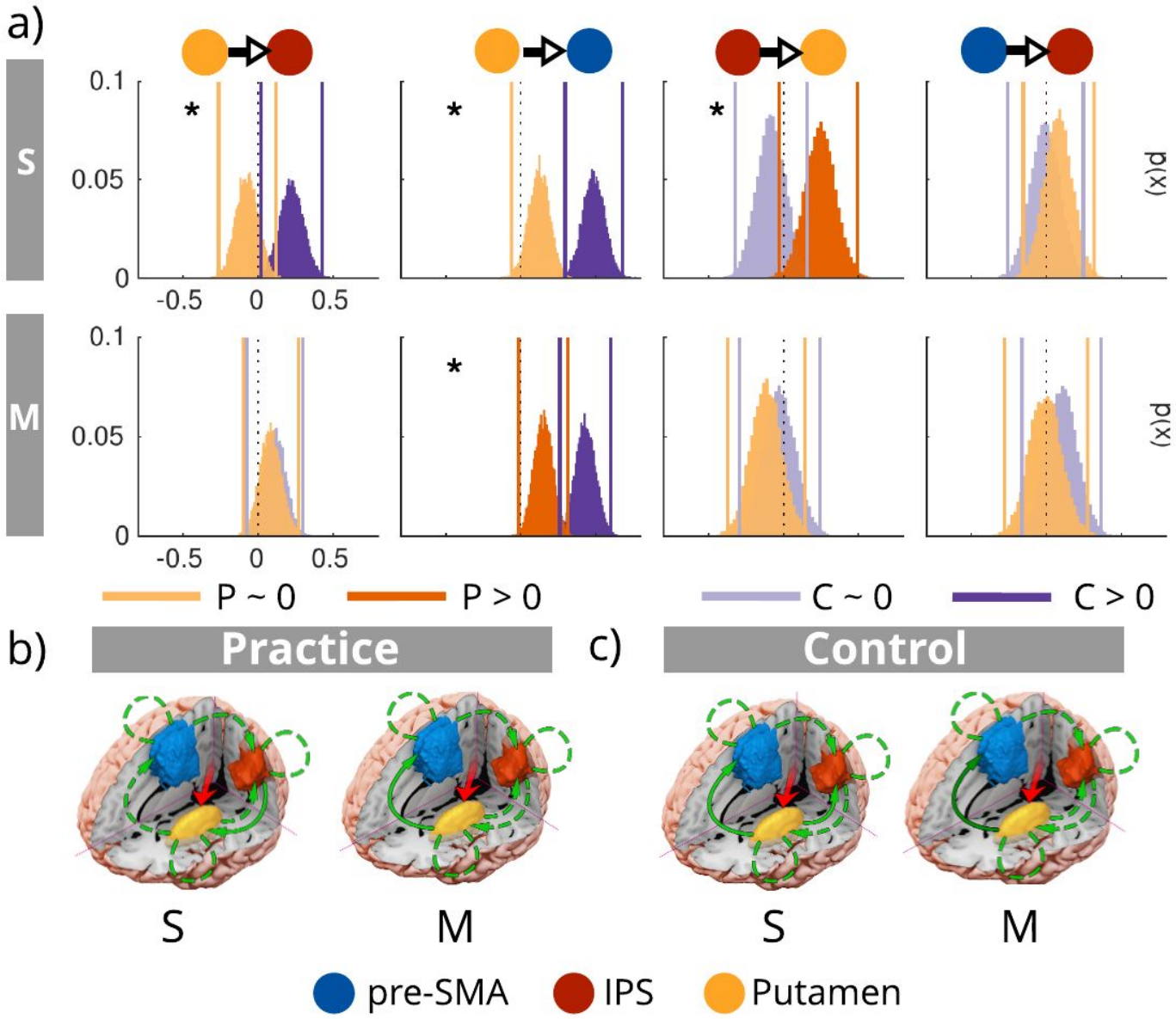
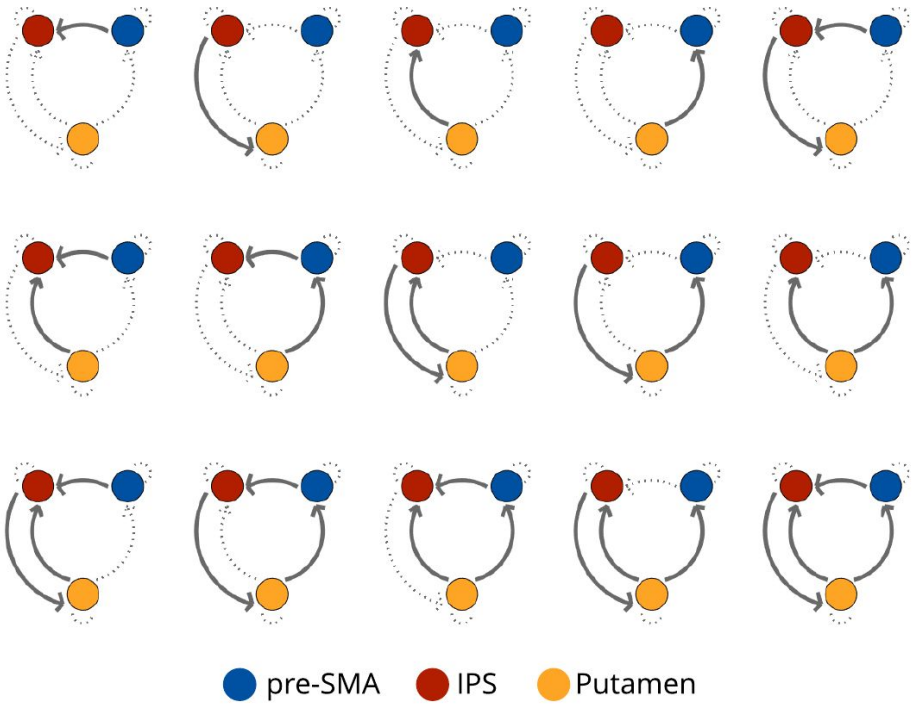
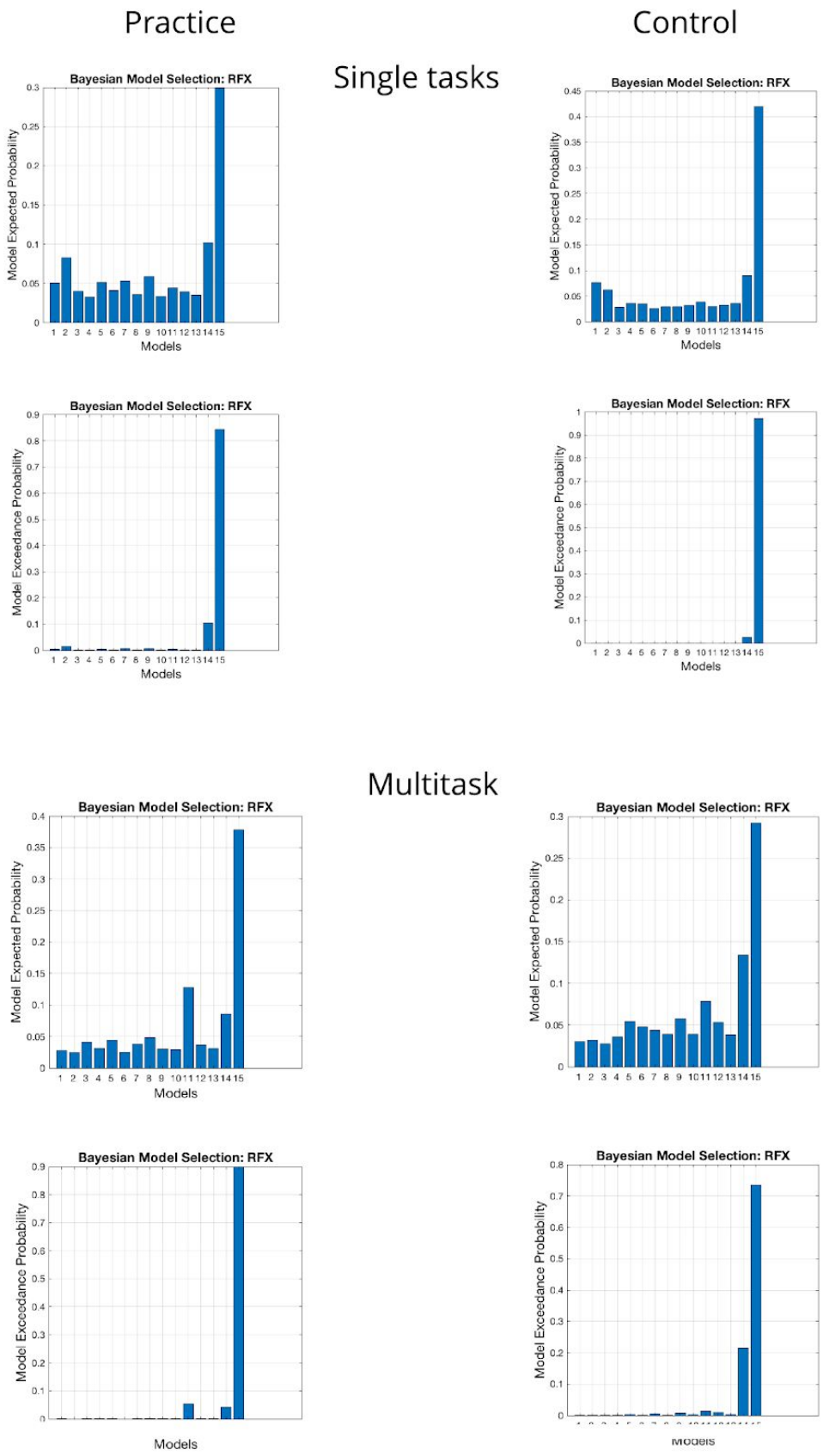


Figure 3: The modulatory influence of practice on the multitasking network. a) Posteriors over parameters were estimated for the practice (P, in orange) and control (C, in violet) groups for single-task trials (S) and for multitask trials (M). Posteriors that deviated reliably from 0 (>0) are in darker shades, whereas those that did not significantly deviate from 0 are in lighter shades. Stars indicate where there were statistically significant group differences. b) Proposed influences of practice on modulatory coupling within the multitasking network for single-task (S) and multitask (M) trials, for the practice and control groups. For multitask trials, the arrows are shaded to indicate the strength of the effect (i.e. the darker the arrow, the larger the modulation to that parameter).



Extended Figure 3a: Model space considered for the modulatory influence of practice (with models *M*=1,..., 15)



Extended Figure 3b: Expected and exceedance model probabilities for single-task (top 4 panels) and for multitask (bottom 4 panels) data for the practice (left column) and control (right column) groups. Models are ordered from 1-15 on the x-axis in the same order as presented in Extended Figure 3a.

Connectivity decreases from Putamen to pre-SMA correlates with lower multitasking costs

Having ascertained that practice modulates striatal-cortical coupling for single tasks and for multitasks, we next sought to understand whether practice related modulations to striatal-cortical coupling were interdependent with behavioural performance improvements. To achieve this, we first calculated the percent reduction of RT in the single task, ΔRT_S from pre- to post- practice):

$$\Delta RT_S = \frac{RT_{S,post}}{RT_{S,pre}} \times 100 \quad (1)$$

With

$$RT_S = RT_{S,V} + RT_{S,A} \quad (2)$$

where VM = visual-manual, AM = auditory-manual and ST = single task. The lower the score, the larger the reduction in RT at post, relative to pre. We then performed Spearman's correlations with the participant specific B parameters from the connections shown to be modulated by practice on single task trials (IPS to Put, Put to IPS, Put to pre-SMA), applying the Sidak adjustment for multiple comparisons. There was a statistically significant relationship between Put to pre-SMA and percent reduction of RT on single trials ΔRT_S ($r_s(93) = .25$, $p = .015$). Interestingly, examination of the correlation data (Figure 4) shows that individuals who showed the largest decreases in Put to pre-SMA coupling showed the largest % reductions in RT performance.

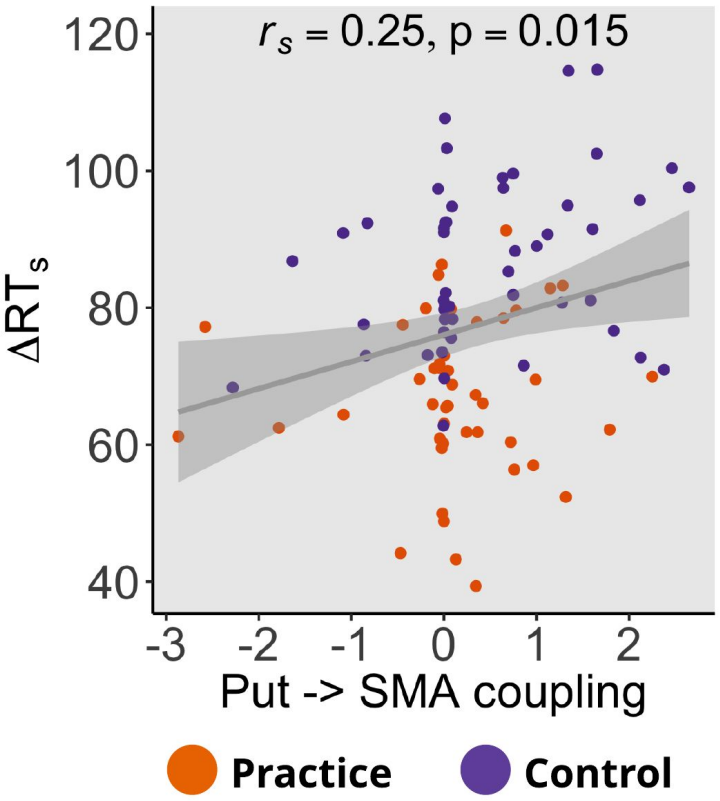


Figure 4: Showing correlation between % reduction in single task (S) response time (RT), relative to pre-practice, and practice related modulations to Putamen to SMA coupling. Individuals who showed the largest decreases in Put to pre-SMA coupling showed the largest % reductions in RT performance.

This relationship also held when we tested for the interdependence between practice related reductions in multitasking costs and modulations of Put to pre-SMA coupling. Percent reduction in multitasking (M) costs, ΔM_{Cost} were calculated as:

$$\Delta M_{Cost} = \frac{(RT_M - RT_S)_{post}}{(RT_M - RT_S)_{pre}} \times 100$$

Where

$$RT_M = RT_{M,V} + RT_{M,A} \tag{4}$$

And RT_S as defined in Eq (2).

Similarly to single task performance, those who showed decreased modulations in Put to pre-SMA coupling, also showed the lowest multitasking costs at post, relative to pre-practice performance ($r_s(93)$ = .26, p=.01, see Figure 5). Thus, reductions in the speed of single-task and multitask performance are both related to decreased rates of information sharing from Put to pre-SMA.

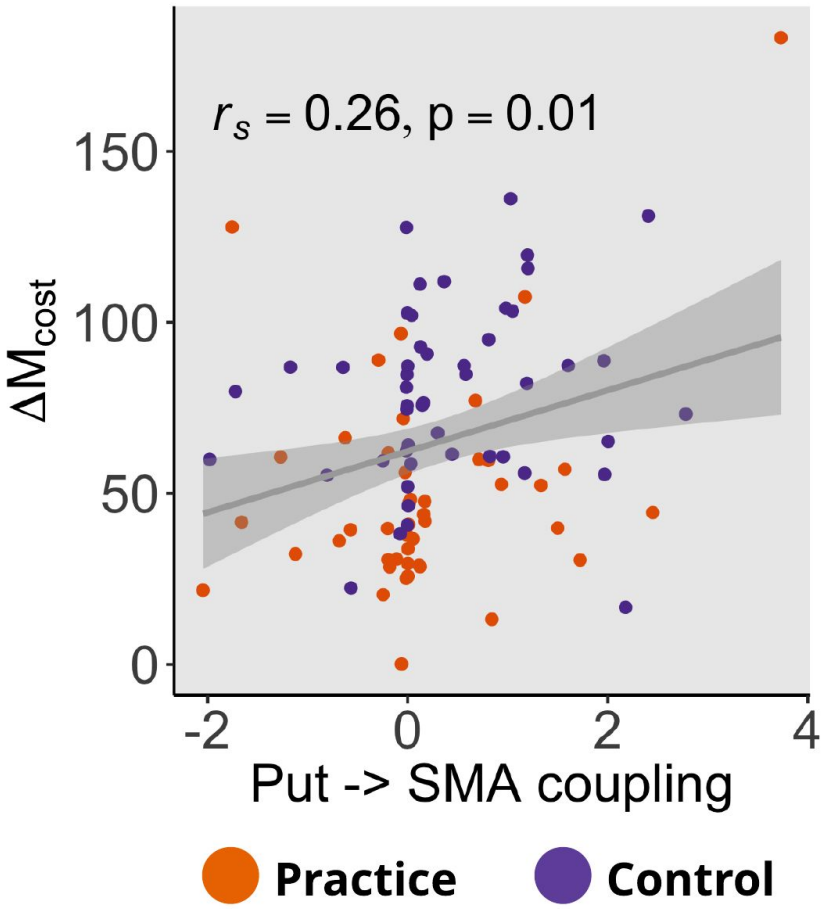


Figure 5: Showing correlation between % reduction in multitask costs (MT), relative to pre-practice, and practice related modulations of Putamen to SMA coupling. Reductions in the speed of single-task and multitask performance are related to decreased rates of information sharing from Put to pre-SMA.

Discussion

We sought to understand how multitasking demands modulate underlying network dynamics, and how practice changes this network to reduce multitasking costs. We asked whether multitasking demands modulated connectivity within a frontal-parietal cortical network, as has been previously assumed (Dux et al. 2006; Marti, King, and Dehaene 2015; Marois and Ivanoff 2005; Sigman and Dehaene 2008; Erickson et al. 2007; Hesselmann, Flandin, and Dehaene 2011; Tombu et al. 2011; Jiang 2004; Watanabe and Funahashi 2014), or whether multitasking modulates the striatal-cortical connections recently implicated as critical in single sensorimotor decision making tasks (Caballero, Humphries, and Gurney 2018; Yartsev et al. 2018; Badre and Nee 2018). Specifically, having previously identified that practice-related improvements correlate with activity changes in the pre-SMA, the IPS and the putamen (Garner and Dux 2015), we applied DCM to ask how multitasking modulates connectivity between these regions. We show that, under multitask relative to single-task conditions, the network is driven via inputs to the putamen, and that multitasking specifically modulates striatal-cortical connectivity, namely; putamen to IPS, and potentially, putamen to pre-SMA. We did not observe evidence that connections between pre-SMA and IPS were modulated by multitasking demands. Therefore, multitasking costs appear to reflect capacity limitations of a different network than has been implied by previous studies focusing on cortical (frontal-parietal) brain regions only. Rather, our results accord with models of single-task decision making that implicate a distributed network that also includes the striatum, in addition to cortical areas. Our results build upon this work by specifically showing that multitasking performance is supported by increased rates of information sharing from striatal to cortical areas. These results strongly imply that limitations in striatal-cortical information sharing underpin multitasking limitations.

We then asked how practice modulated the network dynamics of the proposed multitasking network. Comparable to the finding above, we observed that practice influenced striatal-cortical connectivity. For single-tasks, the control group showed increased couplings from the putamen to IPS, and from the putamen to the pre-SMA. In contrast, the practice group showed increased coupling from the IPS to the putamen. For both groups, the practice factor modulated putamen to pre-SMA connectivity on multitasking trials, but more so for the control group. Subsequent correlation analysis showed that those who had decreased coupling between these regions showed the largest performance improvements. Again, these results show that multitasking limitations are better characterised as stemming from constraints in information transfer from striatal to cortical regions, rather than from limitations in a frontal-parietal network. We now consider the implications of our key findings in turn.

Network dynamics limit to cognitive performance in multitasking - implications

We found that during multitasking, the underlying network is driven by inputs to the putamen, and that while information is propagated between cortical and subcortical areas, multitasking specifically

modulates coupling from the putamen to IPS, and more hesitantly, from putamen to pre-SMA. The IPS is assumed to contribute to the representation of stimulus-response mappings (Pho et al. 2018; Goard et al. 2016; Bunge et al. 2002), and the pre-SMA is assumed to both arbitrate between competitive representations of action-plans (Nachev et al. 2007). Thus both regions potentially constitute key nodes in the cortical representation of a stimulus-response conjunction. We propose that multitasking limitations stem from constraints on the rate at which the striatum can, on the basis of incoming sensory information, sufficiently excite the appropriate cortical representations of stimulus-response mappings to reach a threshold for action. This leads to the intriguing possibility that previous observations that cognitive control operations are underpinned by a frontal-parietal network (Duncan 2013; Watanabe and Funahashi 2014; Dux et al. 2009; Cole et al. 2013) may actually have been observing the cortical response to striatally mediated excitatory signals. In fact, our findings are in line with a recent application of meta-analytic connectivity modelling showing that when frontal-parietal regions associated with cognitive control operations are used as seed regions, the left and right putamen are likely to show significant co-activations across a range of sensorimotor and perceptual tasks (Camilleri et al. 2018). Taken together, these data suggest that the striatum, or at least the putamen, should be included in the set of brain regions that contribute to cognitive control, at least during sensorimotor decision-making.

It was perhaps surprising that the network did not receive driving inputs via IPS, given its association to the dorsal attention system (Corbetta and Shulman 2002; Vossel, Geng, and Fink 2014; Anderson et al. 2010). Furthermore, although pre-SMA showed endogenous coupling with IPS during multitasking, we did not find evidence for reciprocal information transfer between these regions. Additionally, neither multitasking nor practice was not shown to modulate coupling between pre-SMA and IPS. This suggests that although information transfer occurs from pre-SMA to IPS during multitasking, coupling activity between these nodes is not a bottleneck of information processing that gives rise to multitasking costs, and thus may also not be critical for sensorimotor translation. We think our current findings are in keeping with recent demonstrations that while monkey parietal activity correlates with sensorimotor decision-making, it is not impaired by inactivation of the same neurons (Katz et al. 2016). In contrast, ablation of the rat striatum does impair sensorimotor decision-making (Yartsev et al. 2018). As pre-SMA has been recently proposed as contributing to the integration of sequential elements into a higher-order representation (Cona and Semenza 2017), presumably representing the joint probability of the current and upcoming elements. We speculate that endogenous pre-SMA to IPS coupling reflects a biasing of IPS towards likely upcoming choice representations, presumably reinforced by corresponding sensory information transmitted from the putamen. An interesting question that falls out of this interpretation begs what would this be for, if not to perform the current sensorimotor translation? Since recent models of parietal activity indicate timescales of self-excitation that extend beyond the duration of the current sensorimotor translation (Park et al. 2014), one possibility is that the IPS aggregates information over time to guide behaviour in novel but similar contexts. Another possibility, implicated by our findings regarding the influence of practice (see below), is that the IPS aggregates information to support striatal activation of motor plans in the context of well-learned behaviours.

Implications of practice induced plasticity in remediating multitasking costs

An advantage to the current work is that we can both model the dynamics of the network that underpins multitasking limitations, and also identify which couplings are modulated by practice, for both single-tasks and for multitasks. By comparing this to modulations observed in the control group, we can make inroads to identifying which couplings not only correspond to multitasking limitations, but also those that may be critical in determining the extent of their presence and remediation due to practice. We observed that for single-task trials, the practice group showed practice related increases in IPS to putamen coupling, whereas the control group, who were repeating the task after having practiced a regimen not expected to improve multitasking (Garner, Tombu, and Dux 2014; Verghese et al. 2017; Garner, Lynch, and Dux 2016), showed increases in putamen to IPS coupling, and putamen to pre-SMA coupling. We interpret the control group as showing modulations that occur as a consequence of being at an earlier stage of practice (i.e. repeating the task for a second time) than the practice group (who are repeating the task for the 5th time). Taken this way, the current results reflect that initially, practice of single sensorimotor tasks causes an increase in striatal excitation of the cortex, whereas in the longer term, practice causes cortical areas that encode the stimulus-response mapping (specifically IPS) to exert a stronger excitatory influence on the striatum (i.e. putamen more specifically). This is in keeping with recent theories of automatic behaviours positing that the striatum acts to reinforce cortical representations early in learning, and that automatised behaviour involves a shift from striatal to cortical control (Hélie, Ell, and Ashby 2015; Ashby, Turner, and Horvitz 2010). However, our results speak against the suggestion from these theories that automatised behaviour is mediated fully by frontal-parietal (i.e. corticocortical) connections (Hélie, Ell, and Ashby 2015), as we observed no practice related modulations of corticocortical connectivity.

For multitask trials, we observe that being at an earlier stage of practice causes increases in the rate of information transfer from putamen to pre-SMA, and that later stages are associated with a smaller increase of information transfer between these regions. Furthermore, those with the lowest rates of information transfer showed the greatest reductions in both multitask performance costs and single-task response times. We believe these results reflect a trajectory of practice induced changes in putamen to pre-SMA coupling. Therefore, practice reduces multitasking costs in concert with an initial increase, and then a decreased rate of information transmission from putamen to pre-SMA. Rodent studies consistently demonstrate that when a task is novel, firing in the dorsolateral striatum corresponds to the full duration of a trial, whereas as the behaviour becomes habitual, firing patterns transition to coincide with the beginning and end of chunked action sequences (Jin and Costa 2010; Smith and Graybiel 2013; Thorn et al. 2010; Barnes et al. 2005; Jog et al. 1999). Given this, we speculate that our current results comparably reflect that those individuals with the smallest rate of striatal firing (i.e. those that are transitioning towards bracketing activity), show most benefits for multitasking performance. As participants from the practice group showed increases of IPS to putamen coupling on single-tasks, it may be that the shift towards striatal bracketing of task performance is mediated by increased excitation from cortical stimulus-response representations that have been cached over long term learning. Critically, our results clearly show that

multitasking costs can be alleviated by changing the rate of information transfer from the striatum to the pre-SMA.

Interestingly, the current pattern of results, where the practice-induced plasticity on multitask trials is the same for both the practice and the control groups, and practice-induced plasticity on single-task trials is different between groups, suggests that practice does not remediate multitasking costs by improving something extra to the component tasks, such as task-coordination or attention allocation (Strobach and Torsten 2017), but rather, practice changes the circuitry underlying single-task processing, which benefits performance under multitask conditions, thereby reducing information sharing along pathways assumed to be engaged in the excitation of action plans (Forstmann et al. 2008; Haber 2016; Badre and Nee 2018).

Further considerations

It is worthwhile to consider why the previous fMRI investigations into the neural sources of multitasking limitations did not implicate a role for the striatum. As far as we can observe, our sample size, and thus statistical power to observe smaller effects is substantially larger than previous efforts (our N=100, previous work N range: 9-35, (Stelzel et al. 2006; Borst et al. 2010; Tombu et al. 2011; Marois et al. 2006; Jiang 2004; Szameitat et al. 2002; Sigman and Dehaene 2008; Hesselmann, Flandin, and Dehaene 2011; Jiang, Saxe, and Kanwisher 2004; Szameitat et al. 2006; Nijboer et al. 2014; Erickson et al. 2007; Dux et al. 2009, 2006)). One fMRI study has reported increased striatal activity when there is a higher probability of short temporal overlap between tasks (Yildiz and Beste 2015). Moreover, meta-analytic efforts into the connectivity of the frontal-parietal network during cognitive control tasks implicate the putamen (Camilleri et al. 2018). Lesions of the striatum and not the cerebellum have been shown to correspond to impaired multitasking behaviours (Thoma et al. 2008), and intracranial EEG has revealed that fluctuations in oscillatory ventral striatal activity predicts performance on the attentional blink task (Slagter et al. 2017); a paradigm which is assumed to share overlapping limitations with those revealed by sensorimotor multitasks (Garner, Tombu, and Dux 2014; Marti, King, and Dehaene 2015; Tombu et al. 2011; Zylberberg et al. 2010; Jolicoeur 1998; Arnell and Duncan 2002). Therefore, our findings do converge with more recent efforts that do indeed implicate a role for the striatum in cognitive control. We extend these findings to demonstrate how the striatum and cortex interact to both produce and overcome multitasking limitations.

Of course, we have only examined network dynamics in a few areas of a wider system that correlates with multitasking (Garner and Dux 2015), and we are unable to know whether we observe an interaction in these specific regions because the interaction exists nowhere else, or because the interactions are more readily observable between these regions. For example, it could be that cognitive control is mediated by multiple cortical-striatal loops (Badre and Nee 2018; Haber 2003, 2016). Future work should examine the striatal-cortical interactions that underpin other, dissociable forms of cognitive control, such as response-inhibition (Bender et al. 2016), to determine whether the pattern observed here is specific to multitasking, or is generalisable to other cognitive control contexts. Additionally, for the current study, we utilised simple sensorimotor tasks. The networks underpinning the translation of more complex sensorimotor mappings may well invoke more anterior regions of interest than we observed here (Dux et al.

2006; Badre and Nee 2018; Crittenden and Duncan 2014; Woolgar et al. 2011). It remains to be determined whether the current observations generalise to those scenarios.

Conclusions

We probed the network dynamics underlying multitasking limitations, and asked whether they stem from information processing limitations in the previously hypothesised frontal-parietal network (Watanabe and Funahashi 2014, 2018; Garner and Dux 2015; Marti, King, and Dehaene 2015), or whether they were better characterised as stemming from limits in a striatal-cortical network, as suggested by models probing the neural mechanisms underlying single sensorimotor task performance (Caballero, Humphries, and Gurney 2018; Bornstein and Daw 2011; Joel, Niv, and Ruppin 2002). Using an implementation of DCM, we found evidence that multitasking demands motivate increased rates of information sharing between the putamen and cortical sites, suggesting that performance decrements are due to a limit in the rate at which the putamen can excite appropriate cortical stimulus-response representations. We also observed that these limits are attenuated when practice moderates the rate of information transfer between the striatum and cortical sites assumed to encode representations of action plans. We also find evidence that increased rates of information transfer from cortical nodes to the striatum, gained from practice over multiple days, may be a key mechanism for moderating the degree of information transfer required for the striatum to sufficiently excite cortical action representations under conditions of high cognitive load. These results provide clear empirical evidence that cognitive control operations are striatally mediated, and that limitations in cognitive control operations are moderated by information exchange between the putamen and pre-SMA.

Methods

Participants

The MRI scans of the participants (N=100) previously analysed in (Garner and Dux 2015) were included in the present analysis, apart from the data of 2 participants, for whom some of the scans were corrupted due to experimenter error. The University of Queensland Human Research Ethics Committee approved the study as being within the guidelines of the National Statement on Ethical Conduct in Human Research and all participants gave informed, written consent.

Experimental Protocols

Participants attended six experimental sessions: a familiarization session, two MRI sessions and three behavioural practice sessions. Familiarization sessions were conducted the Friday prior to the week of participation, where participants learned the stimulus-response mappings and completed two short runs of the task. The MRI sessions were conducted to obtain pre-practice (Monday session) and post-practice (Friday session) measures. These sessions were held at the same time of day for each participant. Between the two MRI sessions, participants completed three behavioural practice sessions, where they either practiced the multitasking paradigm (practice group) or the visual-search task (control group). Participants typically completed one practice session per day, although on occasion two practice sessions

were held on the same day to accommodate participants' schedules (when this occurred, the two sessions were administered with a minimum of an hours break between them). Participants also completed an online battery of questionnaires that formed part of a different study.

Behavioural Tasks

All tasks were programmed using Matlab R2010a (Mathworks, Natick, MA) and the Psychophysics Toolbox v3.0.9 extension (23). The familiarization and behavioural training sessions were conducted with a 21-inch, Sony Trinitron CRT monitor and a Macintosh 2.5 GHz Mini computer.

Multitasking Paradigm

For each trial of the multitasking paradigm, participants performed either one (single-task condition) or two (multitask condition) sensorimotor tasks. Both involved a 2-alternative discrimination (2-AD), mapping the two stimuli to two responses. For one task, participants were presented with one of two white shapes that were distinguishable in terms of their smooth or spikey texture, presented on a black screen and subtending approximately 6° of visual angle. The shapes were created using digital sculpting software (Scluptris Alpha 6) and Photoshop CS6. Participants were required to make the appropriate manual button press to the presented shape, using either the first or index finger of either the left or right hand (task/hand assignment was counterbalanced across participants). For the other task, participants responded to one of two complex tones using the first or index finger of the hand that was not assigned to the shape task. The sounds were selected to be easily discriminable from one another. Across both the single-task and multitask trial types, stimuli were presented for 200 ms, and on multitask trials, were presented simultaneously.

Familiarisation Session

During the familiarization session, participants completed two runs of the experimental task. Task runs consisted of 18 trials, divided equally between the three trial types (shape single-task, sound single-task, and multitask trials). The order of trial type presentation was pseudo-randomised. The first run had a *short inter-trial-interval (ITI)* and the trial structure was as follows; an alerting fixation dot, subtending 0.5° of visual angle was presented for 400 ms, followed by the stimulus/stimuli that was presented for 200 ms. Subsequently a smaller fixation dot, subtending 0.25° of visual angle, was presented for 1800 ms, during which participants were required to respond. Participants were instructed to respond as accurately and quickly as possible to all tasks. For the familiarization session only, performance feedback was then presented until the participant hit the spacebar in order to continue the task. For example, if the participant had completed the shape task correctly, they were presented with the message 'You got the shape task right'. If they performed the task incorrectly, the message 'Oh no! You got the shape task wrong' was displayed. On multitask trials; feedback was presented for both tasks. If participants failed to achieve at least 5/6 trials correct for each trial type they repeated the run until this level of accuracy was attained.

The second run familiarized participants with the timing of the paradigm to be used during the MRI sessions - a slow event-related design with a *long ITI*. The alerting fixation was presented for 2000 ms, followed by the 200 ms stimulus presentation, 1800 ms response period and feedback. Subsequently an ITI, during which the smaller fixation dot remained on screen, was presented for 12000 ms.

MRI Sessions

Participants completed six long ITI runs in the scanner, with 18 trials per run (6 of each trial type, pseudo-randomly ordered for each run), for a total of 108 trials for the session. Trial presentation was identical to the long ITI run presented at the familiarization session, except that feedback was not presented at the end of each trial.

Practice Sessions

All participants were informed that they were participating in a study examining how practice improves attention, with the intention that both the practice and control groups would expect their practice regimen to improve performance. The first practice session began with an overview of the goals of the practice regimen; participants were informed that they were required to decrease their response time (RT), while maintaining a high level of accuracy. The second and third sessions began with visual feedback in the form of a line graph, plotting RT performance from the previous practice sessions.

For each session, participants completed 56 blocks of 18 trials, for a total of 1008 trials, resulting in 3024 practice trials overall. To ensure that participants retained familiarity with the timings of the task as presented in the scanner, between 2 and 4 of the blocks in each session used long ITI timings.

The practice group performed the multitasking paradigm, as described above (see Familiarization Session), except that performance feedback was not displayed after each trial. Over the course of practice, participants from this group performed 1008 trials of each trial type (shape single-task, sound single-task, multitask). Participants in the control group went through the identical procedures to the practice group, except that they completed a visual search task instead of the multitasking paradigm. Participants searched for a 'T' target amongst 7, 11, or 15 rotated 'L's' (to either 90° or 270°). Participants indicated whether the target was oriented to 90° or 270°, using the first two fingers of their left or right hand (depending upon handedness). Over the course of the three practice sessions, participants completed 1008 trials for each set size.

For both groups performance feedback showed mean RT (collapsed across the two single-tasks for the practice group, and over the three set-sizes for the control group), and accuracy, for the previous 8 blocks, total points scored, and the RT target for the subsequent 8 blocks. If participants met their RT target for over 90 % of trials, and achieved greater than 90 % accuracy, a new RT target was calculated by taking the 75th percentile of response times recorded over the previous 8 blocks. Furthermore, 2 points were awarded. If participants did not beat their RT target for over 90 % trials, but did maintain greater than 90 % accuracy, 1 point was awarded.

MRI Data Acquisition

Images were acquired using a 3T Siemens Trio MRI scanner (Erlangen, Germany) housed at the Centre for Advanced Imaging at The University of Queensland. Participants lay supine in the scanner and viewed the visual display via rear projection onto a mirror mounted on a 12-channel head coil. A T1-weighted anatomic image was collected after the fourth experimental run of the scanning session (repetition time (TR) = 1.9 s, echo time (TE) = 2.32 ms, flip angle (FA) = 9°, field of view (FOV) = 192 x 230 x 256 mm, resolution = 1 mm^3). Functional T2*-weighted images were acquired parallel to the anterior commissure-posterior commissure plane using a GRE EPI sequence (TR = 2 s, TE = 35 ms, FA = 79 °, FOV = 192 x 192 mm, matrix = 64 x 64, in-plane resolution = 3 x 3 mm). Each volume consisted of 29 slices (thickness = 3 mm,

interslice gap = .5 mm), providing whole brain coverage. We synchronized the stimulus presentation with the acquisition of functional volumes.

MRI Data Analysis

fMRI data were preprocessed using the SPM12 software package (Wellcome Trust Centre for Neuroimaging, London, UK; http://www.fil.ion.ucl.ac.uk/spm). Scans from each subject were corrected for slice timing differences using the middle scan as a reference, realigned using the middle first as a reference, co-registered to the T1 image, spatially normalised into MNI standard space, and smoothed with a Gaussian kernel of 8 mm full-width at half maximum.

Dynamic Causal modelling

To assess the causal direction of information flow between brain regions, we applied Dynamic Causal Modelling (DCM), which maps experimental inputs to the observed fMRI output, via hypothesised modulations to neuronal states that are characterised using a biophysically informed generative model (Friston, Harrison, and Penny 2003). Parameter estimates are expressed as rate constants (i.e. the rate of change of neuronal activity in one area that is associated with activity in another), and are fit using Bayesian parameter estimation.

DCM Implementation

Implementation of DCM requires definition of endogenous connections within the network (A parameters), the modulatory influence of experimental factors (B parameters), and the influence of exogenous/driving inputs into the system (e.g. sensory inputs, C parameters) (Friston, Harrison, and Penny 2003). We implemented separate DCM's to investigate i) the modulatory influence of multitasking on the pre-practice data, and ii) the modulatory influence of practice on the pre- to post-practice data.

To make inferences regarding the modulatory influence of multitasking, we defined our endogenous network as comprising reciprocal connectivity between all three of our ROIs, on the basis of anatomical and functional evidence for connections between all three of them (Cavada and Goldman-Rakic 1989; Luppino et al. 1993; Haber 2016; Alexander, DeLong, and Strick 1986; Wise et al. 1997). To address our theoretically motivated question regarding the locus of modulatory influence of the multitasking, we first implemented all 63 possible combinations of the modulatory influence of the multitasking (i.e. allowing each combination of connections to be modulated by the multitasking factor) and then grouped the model space into 3 families: those that allowed any combination of corticocortical modulations, but not striatal-cortical (*corticocortical family,* with 3 models in total $M_{1\text{-}3}$ = 3), those that allowed the reverse pattern (*striatal-cortical family,* with 15 models in total, $M_{4\text{-}18}$, and those that allowed modulations to both types of connections (*both family*, with 45 models in total, $M_{19\text{-}63}$). As both the IPS and the putamen receive sensory inputs (Vossel, Geng, and Fink 2014; Anderson et al. 2010; Grefkes and Fink 2005; Alloway et al. 2017; Saint-Cyr, Ungerleider, and Desimone 1990; Guo et al. 2018; Reig and Silberberg 2014), we implemented the full set of models [$M_{1\text{-}63}$] with inputs to either the IPS, or to the putamen. Thus we fit a total of 126 (2x63) models to the pre-practice data.

To make inferences regarding the modulatory influence of practice on both single and multi-task conditions, we carried out the following for both the single-task and the multitask data (see below for details on data extraction): based on the endogenous connectivity and locus of driving input identified by the

preceding analysis, we then fit the 15 possible modulatory influences of the practice factor (i.e. pre- to post-practice).

Extraction of fMRI Signals for DCM Analysis

The brain regions of interest (ROIs) were selected by the following steps: first we identified regions that that showed increased activity for both single tasks at the pre-training session, second, we sought which of these showed increased activity for multitask trials relative to single task trials. Lastly, we asked which of these regions also showed a practice (pre vs post) by group interaction (Garner and Dux 2015). The left and right intraparietal sulcus (IPS), left and right putamen, and the supplementary motor area (SMA) were implicated by this interaction. In the interest of reducing the complexity of the model space, and in the absence of evidence to indicate lateralized differences, we included only regions in the left hemisphere and the SMA in the current analysis. For each region, we restricted the initial search radius by anatomically defined ROI masks, and extracted the first eigenvariate of all voxels within a sphere of 4 mm radius centered over the participant specific peak for the initial contrast (increased activity for both single tasks, as in the previous study), adjusted for the effects of interest ($p < .05$, uncorrected). Note: to analyse the modulatory influence of practice on single-task data, we regressed out activity attributable to the multi-task condition at this step. To analyse the modulatory influence of practice on multitask data, we comparably regressed out the single-task data at this step. We created the anatomical masks in standard MNI space using FSL. For the IPS we used the Juelich Histological atlas and for the putamen and the SMA we used the Harvard-Oxford cortical and subcortical atlas. Each time-series was concatenated over the 6 pre-training runs for the first analysis concerning the multitasking network, and over the 6 runs from both pre- and post practice sessions [total runs = 12] for the analysis of the influence of practice, and adjusted for confounds (movement and session regressors) in both cases.

Bayesian Model Comparison and Inference over Parameters

As our hypotheses concerned the modulatory influence of our experimental factors on model characteristics, rather than any specific model *per se*, we implemented random effects bayesian model comparison between model families (Penny et al. 2010), with both family inference and Bayesian model averaging (BMA) as implemented in SPM 12. We opted to use a random effects approach that uses a hierarchical Bayesian model to estimate the parameters of a Dirichlet distribution over all models, to protect against the distortive influence of outliers (Stephan et al. 2009). For each family comparison we report i) the expectation of the posterior probability (i.e. the expected likelihood of obtaining the model family *k*, given the data $p(f_k|Y)$), and ii) the exceedance probability of family *k* being more likely than the alternative family *j*, given the data $p(f_k > f_j |Y)$, see (Penny et al. 2010)).

Upon establishment of the winning family, we sought to identify, post-hoc, which specific parameters were likely, given the data, and when relevant, where there was evidence for group differences. To achieve this, we calculated the posterior probability (Pp) that the posterior density over the given parameter has deviated from zero (or in the case of group differences, whether the difference between posterior estimates has deviated from zero), using the SPM spm_Ncdf.m function. To correct for multiple comparisons, we reported Pp's as having deviated from zero when the likelihood exceeded that set by the Sidak correction $(1 - \alpha)^{1/m}$ where m = the number of null hypotheses being tested. To make inference regarding the

relationship between individual parameter estimates and behaviour, we took the subject-specific modulatory parameter estimates and performed non-parametric correlation tests (Spearman's Rho, r_s), owing to violations of normality in the distribution of subject-specific parameter estimates.

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