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The potential of interleaved TMS-fMRI for linking stimulation-induced changes in task-related activity with behavioral modulations

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ABSTRACT

The simultaneous combination of TMS with fMRI has emerged as a promising means to investigate the direct interaction between stimulation-induced changes at the behavioral and neural activity level. This enables the investigation of whole brain neurobehavioral interactions underlying cognitive disruption or facilitation. Yet to date, the literature on interleaved TMS-fMRI in cognitive neuroscience is sparse and neuromodulatory patterns of different TMS protocols are still poorly understood. Here, we synthesize interleaved TMS-fMRI studies on the relationship between direct stimulation-induced changes on task related neural activity and behavior. The following main findings are discussed. First, approximately half of the studies report a relationship between neural activity and behavioral changes as a marker for network excitation or inhibition. Secondly, task difficulty and stimulation timing are crucial factors that impact the interaction between neural activity changes and behavior. Third, stimulation-induced changes in remote, connected areas seem to be stronger associated with facilitation effects at the behavioral level. A better understanding of the relationship between stimulation-induced changes at the neural and behavioral level will increase the current understanding of the neuromodulatory potential of TMS at different levels and may help to develop more efficient stimulation protocols for basic and applied research.

1. Introduction

Transcranial magnetic stimulation (TMS) and functional magnetic resonance imaging (fMRI) are invaluable tools in basic research as well as therapeutic and diagnostic applications. Whereas TMS was introduced as a means to create transient and long-lasting changes in corticospinal excitability and neural activity, fMRI has the potential to map such stimulation-induced changes with a high spatial resolution. Consequently, the combination of both techniques is increasingly being used to modulate and map brain functions.

Interleaved TMS-fMRI refers to the simultaneous integration of TMS with fMRI, combining the non-invasive imaging possibilities of fMRI with the advantages of causal neuromodulation [1–8]. When paired with a task, this approach has the potential to reveal direct network effects associated with modulations in task performance.

While subsequent combinations of TMS with fMRI are better suited to map after-effects of plasticity-inducing stimulation protocols, and provide insight into short-term reorganization and adaptive plasticity (e.g., Ref. [9]), the concurrent combination provides the advantage of elucidating direct consequences of the stimulation at the neural and behavioral level. Yet, the simultaneous combination of both methods is technically challenging and the field is progressing slowly (reflected in only around 78 publications as of April 2021; [10]). While most interleaved TMS-fMRI studies investigated the influence of TMS without a concurrent task, the application of TMS-fMRI during cognitive processing provides the unique opportunity to address, both, open questions regarding the state-dependent mechanism-of-action of TMS as well as cognitive processing itself. To this end, TMS might be leveraged for (1) the evaluation of cortical excitability during task processing (2) disruption of specific neurobehavioral processes or (3) facilitation of specific neurobehavioral processes [11].

More specifically, interleaved TMS-fMRI during task processing might provide optimized readouts for the evaluation of cortical excitability outside the primary motor cortex (M1). Outside the scanner, TMS has already been applied during task processing in the visual domain in some studies to probe excitability patterns beyond M1 [12,13]. However, these studies showed mixed results. Interleaved TMS-fMRI may help to understand the neural underpinnings of increased stimulation

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intensity during task performance and could thus contribute to a better understanding of cortical excitability patterns beyond M1. Regarding the impact of disruptive or facilitatory effects, concurrent imaging has the potential to unravel immediate network effects or compensatory mechanisms of the brain. Moreover, interleaved TMS-fMRI provides a unique possibility to evaluate the role of downstream regions, which are not directly accessible with TMS (e.g., hippocampus or anterior cingulate cortex) and cortical areas compensating for disruption (e.g., contralateral homologous areas; [14]). Identifying immediate network effects may help to select stimulation targets for network disorders such as depression and stroke. In particular, the immediate quantification of network effects provides the unique opportunity to inform targeting by maximizing the stimulation effect in the network of interest while avoiding co-stimulation of non-target areas. A major advantage over task-free interleaved TMS-fMRI applications is the quantification of direct relationships between behavioral readouts (task performance) and physiological readouts (BOLD-response).

Interleaved TMS-fMRI during task processing might therefore critically contribute to the field of basic research and also advance the current understanding and treatment of clinical conditions.

Despite these advantages, the current literature is sparse and heterogeneous. This is likely due to the still widely exploratory nature of this method, the technical challenges of concurrent combinations, and the additional challenges of adding a task on top. Consequently, a thorough synthesis of the existing literature is even more crucial to maximize the gain from lengthy and demanding interleaved TMS-fMRI experiments and inform future experimental and therapeutic applications.

Since 2021, three reviews have been published that discuss different aspects of interleaved TMS-fMRI: 1. Bergmann et al. [14] discuss technical challenges and solutions and provide a comprehensive literature review of the work published until then, 2. Mizutani-Tiebel et al. [10] released an educational review on topics, technical challenges and overview of the literature, and 3. Rafiei & Rahnev [15] investigated local BOLD changes during interleaved TMS-fMRI, attributing them to re-afferent feedback loops.

The aim of this review is to elucidate the relationship between changes in task-related neural activity and behavior during interleaved TMS-fMRI to identify general adaptive mechanisms in response to excitation and inhibition and the relevance of such changes for cognitive processes. Moreover, we aim at identifying effective methodological approaches that successfully modulate both neural activity as well as behavior. These data are synthesized to provide conclusions on brain-behavior interactions, large-scale network interactions and suggestions for future research and application.

2. Methods

Four databases were searched from inception to April 19, 2023: PubMed, Web of Science, PsychInfo and Embase. We used the following search terms: (“transcranial magnetic stimulation” OR TMS OR rTMS) AND (“functional magnetic resonance imag*” OR “functional MRI” OR fMRI OR “functional connectivity” OR fcMRI OR “resting-state” OR “resting state” OR rsMRI OR rsfMRI) AND (task) AND (concurrent OR interleaved OR simultaneous OR synchro*) [10]. The search revealed 277 records of which 152 went into screening after duplicate removal [16]. Finally, 17 studies met the inclusion criteria for our review: original research articles in English language, performance of TMS-fMRI during a task, behavioral results of the task are quantified in the study. A detailed description of study selection can be found in the Supplement.

3. Results

Table 1 and Fig. 1 summarize all included studies per domain. For a comprehensive description of studies, please refer to the Supplementary Information.

4. Synthesizing TMS effects on cognition - how do modulations in task-related neural activity and behavior relate?

Half of the included studies found behavioral changes that were either coinciding or directly correlated with changes in task-related activity. A summary of the results’ synthesis can be found in Fig. 2. Changes in Blood-Oxygenation-Level Dependent (BOLD) response could either indicate disruption of the cognitive process [17,20,25,27] or facilitation [19,31–33]. Specifically, Sack et al. [17] found a relationship between neural activity decrease in the targeted right superior parietal lobule (SPL) and middle frontal gyrus (MFG) and delayed reaction times, indicating that BOLD decrease in local and connected areas is at the core of stimulation-induced performance impairments during visual attention. Raffin et al. [27] reported neural activity increases in the posterior parietal cortex (PPC) for late but not early onset primary visual cortex (V1) stimulation, while only early onset stimulation resulted in a significant decrease in accuracy, potentially indicating network effects underlying performance disruption in the visual domain. On the other hand, in Heinen et al. [20], impaired task performance (inverse efficiency scores) was associated with neural activity increase in stimulated and connected areas during voluntary selective attention.

The memory studies resulting in cognitive improvement discussed here were all characterized by stimulation-induced neural activity increase in remote areas, especially in the temporal lobe. In the study by Webler et al. [33], neural activity decreases in STG were additionally related with performance improvement. In the parietal cortex study [32], enhancement was associated with downstream hippocampus activation increase. The observed enhancement effects at the behavioral level in the above-discussed studies may be explained by priming effects of the stimulation [46–48], that is, TMS may have pre-activated the targeted area to a level that was optimal for task performance. In addition to memory studies, research on attention has also demonstrated a link between performance enhancement and BOLD changes. Heinen et al. [19], found that an increase in contralateral task-related activity was associated with better performance and attentional switching.

In summary, it remains still unclear how BOLD responses reflect TMS effects during task performance, indicating either facilitation or disruption. However, facilitation effects have not been associated with local changes in BOLD response so far. In contrast, these effects were always related to remote network changes. The observed heterogeneity across studies might be explained by differences in the tasks, including required cognitive resources and demands as well as the TMS protocol and the statistical approaches performed in the respective studies. Consequently, it is too early to make strong predictions about the direction of the interaction of immediate TMS effects on task-related activity and behavior that generalize across cognitive domains. Most of the studies have found changes in neural response due to stimulation during task processing. However, this was not always related to measurable performance changes. While most neural changes might be associated with within-network effects of the respective target networks, some activation changes might have been due to interactions with peripheral effects (see below).

In the following, we provide suggestions for the sources of outcome variability during task-based interleaved TMS-fMRI which may guide the planning and interpretation of future studies. We note that task selection and stimulation timing are strongly tied to state-dependent TMS responses [49,50].

Table 1
Study characteristics.

Domain	Study	n	Task	TMS design					Outcomes		
				Target	Stimulation Protocol	Stimulation Intensity	Interleaving	Control Conditions	fMRI Outcome	Behavioral Outcome	Interactions
Attention	[17]	8	angle/color discrimination in visual clock paradigm (block design)	r. parietal cortex, l. parietal cortex (1 cm posterior to P3 and P4)	~13.3 Hz; 5 pulses; simultaneously with stimulus onset, stimulation at each trial	100 % MSO (126 % MT on average)	TR = 2 s, 560 ms volume gap	noTMS; noTask (TMS + fixation); different side	TMS > noTMS: BOLD decrease in right SPL and MFG for right side stimulation in angle task; BOLD increase mainly in M1 and A1 areas;	r. parietal TMS prolonged RT during angle task	right SPL/MFG BOLD decrease and RT increase
	[18]	8 recruited; 6 included	covert sustained visuospatial attention to checkerboards; counting deviant tiles on left or right checkerboards based on initial cue at the beginning of block (block design)	right PPC (22 -60 60, MNI)	10 Hz; 5 pulses; simultaneously with stimulus onset; stimulation at each trial	75 and 35 % MSO	TR = 3 s, 570 ms volume gap	different task conditions (left, right, neutral); low intensity TMS	increased BOLD response for left attention in right occipito-temporal cortex; increased BOLD response for right attention in left occipito-temporal cortex;	no influence of TMS on RTs or accuracy	none
	[19]	12 recruited; 11 included; 5 participated in interleaved TMS-fMRI	cued spatial attention and visual discrimination task with 50 % invalid cues (event-related)	right AG (40 -73 44, MNI); vertex (0 -34 78, MNI)	11 Hz; 3 pulses; 90 ms after stimulus onset; stimulation at each trial	40 and 120 % MT	TR = 2.52 s; pulses applied between the EPI navigator echoes and the EPI data readout; slices acquired next to a pulse were interpolated	low intensity TMS; different task conditions (left, right); vertex stimulation	increased BOLD response for invalidly cued right targets at high intensity TMS in the left AG;	increase in accuracy for right hemifield targets for invalidly cued targets (high intensity TMS); decrease in accuracy for validly cued targets	%-signal change increase goes along with increased accuracy for invalidly cued targets in the right hemifield
	[20]	16; 3 excluded from behavioural analysis	cued visual attention task: attent to visual motion, sex of faces or passive viewing (event-related)	right FEF (31 1 58, MNI)	11 Hz; 3 pulses; 40 ms after stimulus onset; stimulation at each trial	40 and 110 % MT	TR = 2.97 s; pulses applied between the EPI navigator echoes and the EPI data readout; slices acquired next to a pulse were interpolated	low intensity TMS; different task conditions (focus on sex, motion, passive);	bilateral increase in %-signal change in bilateral FEF; increased %-signal change for left MT+ for motion condition; increased %-signal change for bilateral FFA for sex condition;	high intensity TMS hampered performance in visual motion condition	significant correlation between increased %-signal change in rFEF and left MT+ and hampered task-performance for motion discrimination
	[21]	10	sustained visual attention paradigm with or without task irrelevant auditory stimulus for weak visual stimulus (block/ event-related)	right IPS (34.1 -50.7 64.3, MNI)	10 Hz; 4 pulses; 100 ms after stimulus onset; stimulation at each trial	69 % MSO (125 % of average rMT)	TR = 3.29 s; 600 ms volume gap	sham TMS (2 cm thick distance plate between coil and scalp)	TMS led to BOLD increases in rSPL, PCG & PCL; interaction effect between auditory present and auditory absent in right middle temporal gyrus and left insula	no behavioural effect of TMS	none; not intended by authors
	[22]	same as [21]	same as [21]	same as [21]	same as [21]	same as [21]	same as [21]	same as [21]	same as [21]	same as [21]	same as [21]

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Table 1 (*continued*)

Domain	Study	n	Task	TMS design					Outcomes		
				Target	Stimulation Protocol	Stimulation Intensity	Interleaving	Control Conditions	fMRI Outcome	Behavioral Outcome	Interactions
	[23]	31 signed up; 20 finished all sessions	perceptually difficult feature processing (color, shape) of two abstract shapes; congruent vs. incongruent button press sides over conditions (block design)	right DLPFC (44 31 28, MNI)	13 Hz; 3 pulses; 75 ms after stimulus onset; stimulation at each trial	40 and 110 % MT	TR = 2.45 s; sacrifising one slice	low intensity TMS; different task conditions (discriminate shape or color)	active TMS led to BOLD increases in lDLPFC, rV1, lHG, r/lSTG, lSTG, rACC, r/l extratstiate	decreased accuracy for congruent and incongruent trials for real > sham	not investigated
Attention (no behavioural outcome)	[24]	20	visual or auditory cues and cross fixation; participants had to press button for odd stimuli to maintain attention	right IPS (Talairach: 38 -44 46); vertex (MNI: 2 -32.5 4.4)	1.9 Hz	60 % and 120 % mean motor threshold	TR = 2.3 s; slice gap of 110 ms every 425 ms	low intensity TMS; different task conditions; no TMS	increase in BOLD response for visual cortex (cuneus) selectively for IPS stimulation at high intensity	button press served as quality control	NA
Vision	[25]	3	line bisection judgement task (event-related)	right AG in participant 1 (P1, approximate MNI coordinates: 51 -61 51) and participant 3 (P3: 40 -75 44), near intra-parietal sulcus (IPS) in the SPL, in participant 2 (P2: 43 -61 61)	Single pulse (150 ms after stimulus onset); stimulation at each trial	115 % rMT	TR = 2.3 s; between slice stimulation (artifact free)	vertex stimulation: different task conditions; no TMS	parietal > vertex: left pre/post central, IPL, SMG; right pre/ postcentral, STG, AG	RT lower in vertex irrespective of on/ off; rightward judgement bias	judgement bias went along with BOLD decrease in right IPL, SMG, AG, SFG, MFG, left IPL, PCG
	[26]	27	motion perception task (event-related)	Oz	10 Hz; 3 pulses; at stimulus onset; stimulation at each trial	20, 40, 60, 80, 120 % rMT	between slices (slice positioning chosen to avoid artifacts close to stimulated area)	different intensities	increased connectivity between visual and SM and auditory system depending on stimulation intensity	80 % intensity decreased accuracy compared to other intensities; regression model revealed higher accuracy for stronger within network connectivity and lower accuracy for stronger between network connectivity	none
	[27]	16	motion perception task (event-related)	EVA (mean: 8 -76 9), hMT+/V5 (mean: 46 -83 11)	10 Hz; 3 pulses; (60/150 ms delay EVA; 30/130 ms delay hMT+/V5); 1/3 of no TMS trials	around 80 % MSO, around 38 % MSO	TR = 2 s; 570 ms volume gap	different time points; different sites; different intensities	TMSEVA > noTMS: increased local BOLD and in SMA for static and moving dots; TMS hMT+/V5 > noTMS: local BOLD increase and in EVA areas	TMS in EVA with early onset significantly decreased accuracy; TMS in hMT+/V5 with early and late onset significantly decreased accuracy for hMT+/V5	ROI analysis revealed significant increase in PPC beta-estimates for EVA late onset as compared to EVA early onset

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Table 1 (*continued*)

Domain	Study	n	Task	TMS design					Outcomes		
				Target	Stimulation Protocol	Stimulation Intensity	Interleaving	Control Conditions	fMRI Outcome	Behavioral Outcome	Interactions
Vision (no directly observed behavioural outcome)	[5]	4	online: exposure to Gabor stimuli; offline: contrast judgement between Gabor stimuli (central and peripheral exposition)	right FEF (functional localizer); vertex	9 Hz; 5 pulses; 100 ms after stimulus onst	40, 55, 70, 85 % MSO (85 % MSO = ~118 % rMT)	TR = 3 s; 570 ms volume gap	different intensities; different stimulation sites; no stimulus; no TMS;	decreased BOLD response in bilateral occipital pole and increase in bilateral calcarine sulcus as a factor of stimulation intensity; effect stronger for stimulus presentation as compared to blank screen	TMS enhanced perceived contrasts for peripheral stimuli (offline)	not directly investigated; retinotopic mapping might suggest modulation of pripheral vision
	[28]	4 (same as in Ref. [5])	same as in [5]	right IPS (MNI: 36 -52 48)	same as in [5]	same as in [5]	same as in [5]	different intensities; different stimulation sites; no stimulus; no TMS;	decresed BOLD response in V5/MT+ for high-intensity stimulation over right IPS but not FEF	NA	NA
	[29]	4 (same as in Ref. [5])	same as in [5]	left FEF (MNI: -27 -1 57); left IPS (MNI: -36 -48 45)	same as in [5]	same as in [5]	same as in [5]	different intensities; different stimulation sites; no stimulus; no TMS;	no effect for left IPS; left FEF BOLD decrease in bilateral occipital pole	NA	NA
Memory	[30]	16	delayed recognition working memory task (event-related)	right DLPFC (average MNI: 37 36 34)	11 Hz; 3 pulses; 1710 ms after memory target offset, with second distracter for distraction-present trials or at the same timepoint in the unfilled delay period of distraction-absent trials; stimulation at each trial	40 % MT, 110 % MT	TR = 3 s; between slices during readout, sacrificing one slice	different task conditions; different intensities;	BOLD increase 110 % > 40 % FFA ROI for face target with house distracter & PPA ROI for house target face distractor	none	TMS not intended to change behaviour
	[31]	22 recruited,17 included	semantically cued memory encoding task (event-related)	Beam F3 (left DLPFC)	10 Hz; 3 pulses; onsets 200, 600 or 1000 ms after stimulus onset; stimulation at each trial	100 % rMT	TR = 3 s; jittered 20 ms after excitation pulses - > artifacts	diffrent task conditions; different time points;	increased BOLD-response for 600 ms onset in right IFG, left MTG, ACC, left and right occipital	performance better at 600 ms, worse 1000 ms outside the scanner	BOLD changes for related correspond with performance accuracy in right IFG, left MTG and ACC ROIs
	[32]	18 recruited, 16 included	memory encoding task, number decision (odd/even; event-related)	left lateral parietal cortex location (average MNI: -53 -41 27); left SMA	TBS (50Hz bursts at 5 Hz) or 30 beta (12.5 Hz) pulses, 2s before target onset;	80 % rMT	TR (TBS) = 2.23 s, TR (beta) = 2.44 s; between slices	different sites; different frequencies; different task	main effect of TMS in bilateral A1	Better recollection and hippocampus response only after TBS at parietal left stimulation	selective effect of TBS on performance improvement and left anterior

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Table 1 (*continued*)

Domain	Study	n	Task	TMS design					Outcomes		
				Target	Stimulation Protocol	Stimulation Intensity	Interleaving	Control Conditions	fMRI Outcome	Behavioral Outcome	Interactions
				(average MNI: 36 3 67)	mixed on and off trials			conditions; no TMS;			hippocampus BOLD-changes
	[33]	20 recruited, 15 included	n-back (0-back, 2-back; block design)	left DLPFC; F3 according to the 10e20 EEG	7 pulses, separated by 2.4 s; task jittered	100 % rMT	TR = 2.4 s; 150 ms volume gap	different task conditions; no TMS;	2-backTMS > 0-backTMS: PCC, SMG, right STG, right hippocampus, left AG, right TP, left MTG (decrease); left SPL, right IPL, left IFG, right MFG, right SFG (increase)	Increased accuracy 2-back with TMS	increased accuracy during 2-back went along with BOLD-changes during 2-back
	[34]	26 recruited, 20 included	n-back (0-back, 2-back; block design)	left DLPFC; individual anticorrelated ACC target	10 Hz; 3 pulses; 250 ms before or 150 ms after letter onset; delivered at 16 letters	100 % rMT	in between slices	different task conditions; different onsets; no task; no TMS	2-back late vs early > 0-back late vs early: BOLD increase in left IFG/DLPFC; decrease in ACC left caudate and right IPL	worse accuracy for 2-back during early stimulation; higher reaction times in 0-back for late stimulation	NA
Motor	[35]	1 amputee	phantom sense of movement during left M1 stimulation (event-related)	left M1	single pulse; stimulation at each trial	90 %, 98 %, 102 % and 110 % of sense of movement threshold	TR = 2 s; 100 ms gap every 10 slices	different intensities	increased BOLD response in M1 and PMd for sense of moving rating yes > no	MEP in deltoid muscle for 110 % stimulation	NA
	[36]	12	grip, no grip (event-related)	left PMd (-26 -14 62)	11 Hz; 5 pulses; 900 ms after instruction onset	70 % aMT, 110 % rMT	TR = 1.8 s; between slices inducing artifacts	different intensities; different task conditions (on, off)	BOLD increase for TMS during grip in the right M1 and PMd	no significant differences between grip force, duration or onset time	not intended to avoid BOLD changes elicited by behavioural influences
	[37]	12 stroke patients	grip, no grip (event-related)	contralesional PMd	11 Hz; 5 pulses; 900 ms after instruction onset; stimulation at each trial	70 % aMT, 110 % rMT	TR = 1.8 s; between slices inducing artifacts	different intensities; different task conditions (on, off)	BOLD increas in ipsilesional IPL during hand grip at 110 %	no significant differences between grip force, duration or onset time; no contralesional hand movement	not intended to avoid BOLD changes elicited by behavioural influences; higher beta in iIPL during TMs handgrip was associated with worse clinical outcome
Motor (no behavioral task outcomes)	([4])	7 (5 with sig. activation)	volitional movement cued by 20 % MSO stimulation	l. M1	1 Hz; 21 pulses each epoch	20 % MSO (movement cue), 110 % rMT active TMS	TR = 3 s, 12 slices; pulses at 0.1 s, 1.1 s, 2.1 s	rest (no TMS, eyes closed)	volitional movement similar to TMS-induced muscle-response in regions and levels of motor & auditory cortex activation	NA	NA

(*continued on next page*)

Table 1 (*continued*)

Domain	Study	n	Task	TMS design					Outcomes		
				Target	Stimulation Protocol	Stimulation Intensity	Interleaving	Control Conditions	fMRI Outcome	Behavioral Outcome	Interactions
	[38]	11 (6 young, 5 old)	volitional movement cued by 20 % MSO stimulation; listen to clicks	l. M1	1 Hz; 21 pulses each epoch	20 % MSO (movement cue), 110 % rMT active TMS	TR = 3 s, 12 slices; pulses at 0.1 s, 1.1 s, 2.1 s	rest (no TMS, eyes closed)	correlation of activation in volitional movement and TMS-induced muscle-response; for volitional movement and click listening at 20 % MSO, activation old > young	NA	NA
	[39]	11	volitional movement cued by 20 % rMT stimulation	l. M1	1 Hz; 21 pulses each epoch	20 % MSO (movement cue), 110 % rMT active TMS	TR = 3 s, 15 slices; pulses at 0.1 s, 1.1 s, 2.1 s	rest (no TMS, eyes closed)	no diff. in BOLD pattern between TMS- & volitional movement	NA	NA
	[40]	9 (same as [41])	same as [41]	same as [41]	same as [41]	same as [41]	same as [41]	different task conditions	BOLD increase for execution > imagery after TMS in right IFG, dorsal cingulate cortex, bilateral STG, right ITG, bilateral anterior cerebellum, bilateral putamen	NA	NA
	[41]	7 cervical dystonia patients; 9 healthy controls	movement execution; movement imagery; (right hand)	left SPL (MNI: -24 -60 68)	1 Hz; 10 pulses; before task onset	115 % MT	TR = 2.3 s: between slices inducing artifacts	different task conditions; two groups	decreased BOLD in right angular gyrus for patients vs controls for motion execution with TMS > motion execution without TMS	NA	NA
	[42]	36 (12task-M1,12rest-M1,12rest-sham)	self-paced hand clenching (l., r., both), rest	l. M1, r. M1(motor hotspot), vertex (10–20)	11 pulses 1 Hz	100 % rMT	TR = 800 ms + pulse + 800 ms + pulse	rest vertex no TMS (within)	decreased activity in operculum & STG and increasd activity in SPL and precuneus for movement compared to rest;	NA	state dependency: TMS effects greater at rest than task or sham
	[43]	23 (12task, 23rest)	self-paced hand clenching (l., r., both), rest	l. M1(motor hotspot)	11 pulses 1 Hz	100 % rMT	TR = 800 ms + pulse + 800 ms + pulse	rest noTMS	DCM for left hand clench reveals decreased inhibitory connectivity from	NA	NA

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Table 1 (*continued*)

Domain	Study	n	Task	TMS design					Outcomes		
				Target	Stimulation Protocol	Stimulation Intensity	Interleaving	Control Conditions	fMRI Outcome	Behavioral Outcome	Interactions
Motor (continuous arterial spin labeling)	[44]	9	externally cue key press: associative or freely selected finger	left PMd	10 Hz rTMS	70 % aMT, 110 % rMT	TR = 4 s; tag duration = 2.343 s; stimulation during tagging	different task conditions; different stimulation intensities;	insula to M1 for TMS stimulation increase in contralateral M1 & PMd BOLD-response for associative keypress > free keypress	none	none
Emotion	[45]	44 recruited; 41 included	neutral, predictable and unpredictable threat task (block design)	right DLPFC (based on working memory fMRI localizer); IPS	50 Hz; 3 pulses; twice during each block	100 % rMT	TR = 2 s; volume gap	different task conditions; control site	BOLD decrease in right somatomotor; left insula; bilateral SMA ROIs for safe vs. threat stimuli	offline anxiety ratings significantly lower for safe trials	not directly assessed

Abbreviations: MSO = maximum stimulator output, MT = motor threshold, SPL = superior parietal lobule, MFG = middle frontal gyrus, M1 = primary motor cortex, A1 = primary auditory cortex, RT = reaction time, PPC = posterior parietal cortex, Hz = Hertz, AG = angular gyrus, FEF = frontal eye-field, MT+ = medial temporal, FFA = fusiform face area, IPS = intraparietal sulcus, PCG = postcentral gyrus, PCL = paracentral lobule, DLPFC = dorsolateral prefrontal cortex, HG = Heschel's gyrus, STG = superior temporal gyrus, ITG = inferior temporal gyrus V1 = primary visual cortex, ACC = anterior cingulate cortex, SMG = supramarginal gyrus, Oz = occipital central (EEG-position), EVA = early visual area, SMA = supplementary motor area, PPA = parahippocampal place area, MTG = middle temporal gyrus, TBS = theta burst stimulation, SFG = superior frontal gyrus, M1 = primary motor cortex, PMd = dorsal premotor cortex, MEP = motor-evoked potential.

5. Potential sources of variability in neural response-behavior relationships

5.1. Task difficulty and task design

Some of the visual (attention) studies adjusted task difficulty to the participants' visual detection thresholds [27,19,26,21]. Of these, two found neural activity modulations going along with behavioral changes [27,19], one reported significant changes in behavior but only trends towards neural response changes [26], and one study only found changes in neural activity [21]. In the latter study, the employed task might have been too easy to result in stimulation-induced performance modulations. In two other studies, relationships between stimulation-induced neural activity changes and task-impairment were only found in the more difficult of two task conditions, supporting the role of task difficulty in the interaction between behavioral impairment/facilitation and adaptive BOLD changes [20,17]. Accordingly, memory improvement was selectively observed for the more difficult of two conditions in two studies [32,33]. In Hawco et al. [31], on the other hand, the TMS effect only occurred during encoding of semantically related items but not in the semantically unrelated items, indicating that the latter task condition might have been too difficult to differentiate TMS effects. In fact, interactions of TMS effects and task difficulty or participants' individual abilities have been suggested previously [51]. Likewise, task-related neural activity during interleaved TMS-fMRI experiments might be influenced by task difficulty and habituation effects [52,53].

Beyond task difficulty, the task paradigm might influence study results. Some task paradigms, especially those targeting working memory, are inherently designed to be administered in blocks, with stimulation applied at specific time points within these blocks [33,34]. In other experiments, block designs were chosen with stimulation being applied at each trial or in an event-related fashion (see Table 1). For some studies, task-based interleaved TMS-fMRI requires adjustment of timing and task onsets. Specifically, if TMS pulses are given in between volume gaps, the onsets of the individual task trials need to be time-locked to the repetition times (TRs) of the imaging sequence. This in turn might influence resulting activation maps as compared to a standard fMRI session without TMS. Finally, the specific goal of the study should also guide the choice of task: For instance, if the primary aim is to examine modulatory effects at the group level, it may be important to minimize task variability within conditions. Conversely, if the focus is on individual differences in response to specific conditions, greater variability between conditions might be preferable.

Conclusions: If the intention of the TMS session is to investigate the interaction between behavioral modulation and BOLD modulation, it might be advisable to individually adjust task difficulty in task-based TMS-fMRI, especially if there is more than one session (real/sham, multiple sites) to avoid pure habituation effects [52] and ceiling or floor effects which may mask potential TMS effects [54]. Finally, it might be advisable to perform some trials/blocks without TMS to obtain a reference of task activations with the interleaved TMS-fMRI adjusted setup.

5.2. Timing

Timing of TMS pulses or trains is a crucial point in the context of both disruption [55–57] and priming [47] approaches. While most interleaved TMS-fMRI studies introduced fixed delays between sensory stimulus onset and TMS onset, some authors systematically varied stimulation onsets to compare neural response-behavior relationships relative to stimulation onsets [27,31,34]. Such chronometric approaches can provide insights into the relevance of specific task periods and the interaction of different areas across the time course of task processing.

In the study by Hawco et al. [31], TMS over the left DLPFC had an onset-specific effect on semantic memory encoding that was associated

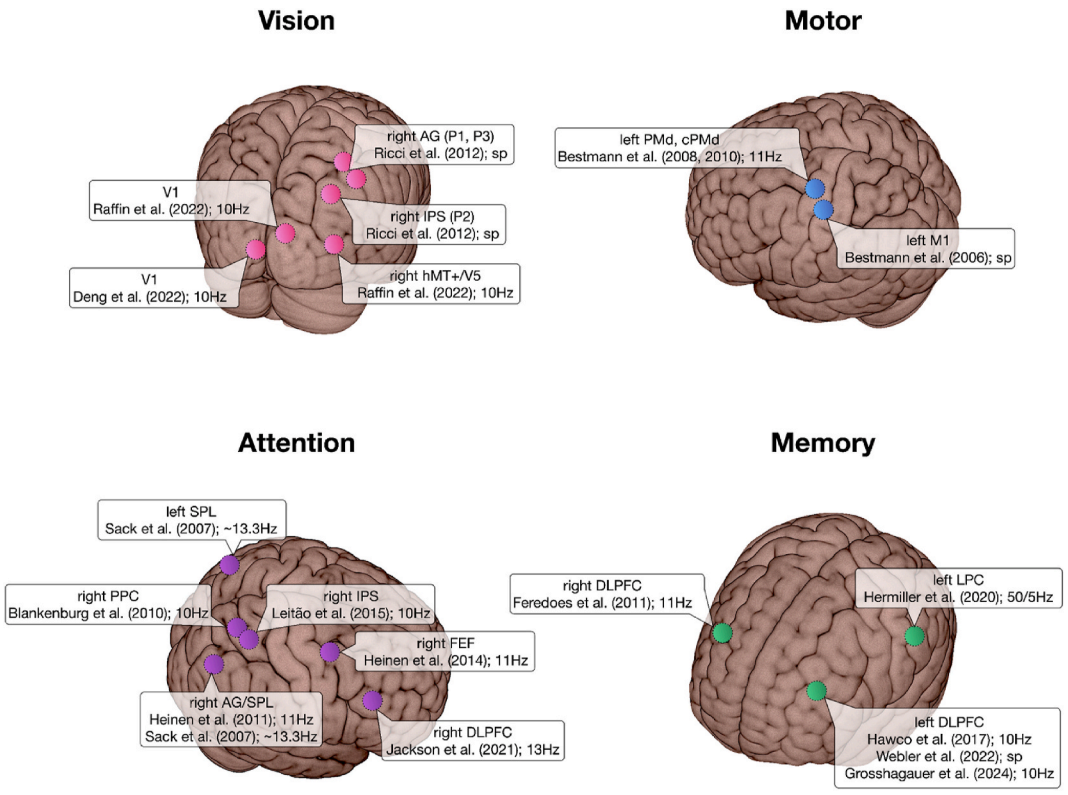


Fig. 1. Overview of the stimulation locations and frequency. Included studies focused on four different domains: vision, motor, attention and memory. While studies on vision and attention mostly targeted the right hemisphere, motor and memory included more left hemispheric targets. Abbreviations: V1 = primary visual cortex, AG = angular gyrus, SPL = superior parietal lobule, IPS = intraparietal sulcus, PMd = dorsal premotor cortex, M1 = primary motor cortex, PPC = posterior parietal cortex, FEF = frontal eye field, DLPFC = dorsolateral prefrontal cortex, LPC = lateral parietal cortex, sp = single pulse.

with BOLD changes. TMS resulted in significant performance decreases only if the stimulation onset was delayed 1000 ms relative to the picture onset, while performance was significantly increased for the 600 ms delay. In another study, Raffin et al. [27] found TMS timing effects over different sites of the visual system (V1, hMT+/V5) during a visual motion paradigm at two time points per site (60/150 ms for V1, 30/130 ms for hMT+/V5) that were also reflected in BOLD changes. In a recent study, Grosshagauer et al. [34] systematically investigated the effect of online TMS relative to letter onset in an n-back paradigm (-250 ms/150 ms). While finding significant BOLD changes, early stimulation led to performance decreases in the 2-back condition. The study by Webler et al. [33] did not specifically control for timing but applied single pulses during an n-back task at arbitrary time points relative to visual stimuli, potentially resulting in priming effects.

Conclusions: Timing seems to have an important effect both on the BOLD response as well as performance modulation during online TMS. Therefore, it might be advisable to pilot the effect of stimulation timing in advance to increase stimulation efficiency. In this context, relative to behavioral TMS studies with chronometric designs, interleaved TMS-fMRI provides the advantage of not only probing the functional relevance of specific areas across the time course of a task, but also elucidating the underlying effects on task-related neural activity. While stimulation before memory encoding may enhance performance via priming [47,50], stimulation during task processing might disrupt this specific process in a time-specific manner [56–58], as suggested in early studies on chronometric TMS approaches [59]. For working memory, single-pulse TMS has also been suggested to reactivate relevant contents during the maintenance phase [60], which may have contributed to enhancement effects in the study by Webler et al. [33].

5.3. Stimulation dose

Another factor that influences both behavioral outcome and BOLD response is the stimulation intensity. In this respect, one interleaved TMS-fMRI study systematically investigated the influence of V1 stimulation on visual motion discrimination as a factor of increasing stimulation intensity [26]. These authors stimulated at 20, 40, 80 and 120 % of the participants' resting motor thresholds. At the behavioral level, they found a decrease in performance accuracy for 80 % stimulation intensity compared to all other intensities. A trend towards decreased within-network-connectivity of the visual network for 80 % stimulation may have reflected the inhibitory influence of the TMS pulses. However, as the authors did not correlate the two measures, it remains unclear if there was a direct relationship between connectivity and behavioral response.

Moreover, it is unclear if stimulation at "in-between intensities", such as 100 %, would have led to a similar effect. In terms of neural activity changes, the authors found an increase in between-network-connectivity between the visual and sensory-motor/temporal lobe networks at 120 % stimulation intensity, which was not associated with any behavioral effect. These observations might be due to the stronger influence of peripheral effects, that is, louder clicking and stronger sensations [61,62], given the specific between-network effects for temporal and sensory-motor networks. Another caveat when investigating different intensities is the inherent intensity-focality trade-off. Higher stimulation intensities not only result in deeper penetration of cortical areas, engaging more cell layers, but also co-stimulate a larger cortical area. This broader activation may lead to qualitatively different TMS outcomes. For example, at 120 % stimulation intensity, additional brain areas may be co-stimulated, potentially producing stimulation effects that oppose those intended from the primarily targeted area [63].

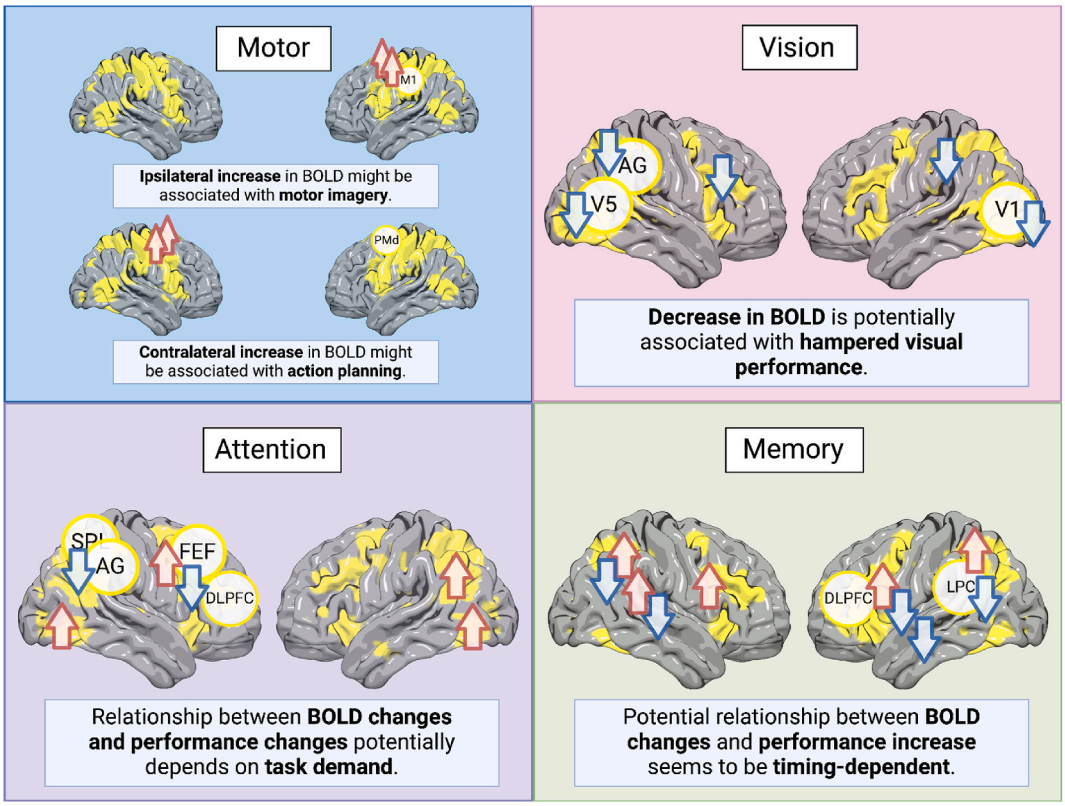


Fig. 2. Potential relationships between BOLD and performance changes. ***Upper Left (Motor):*** While TMS-evoked perception of hand movement seems to be indicative for ipsilateral activity increase, task interference during a motor task seems to increase contralateral BOLD response. Summarized based on Bestmann et al. [35–37]. ***Upper Right (Vision):*** Available studies suggest a decrease in BOLD response to be associated with impaired visual performance. ***Lower Left (Attention):*** Available studies suggest a modulation in BOLD response to be associated with modulations in attention performance mediated by task demand. ***Lower Right (Memory):*** Available studies suggest a modulation in BOLD response to be associated with improvement in memory performance mediated by TMS timing and *task demand.*

Stimulation targets for all domains are marked as circles (yellow border). Activity increase is depicted by red arrows while decrease is depicted by blue arrows, the addressed respective networks ('hand movements', 'visual', 'attention network', and 'memory' search terms neurosynth (Yarkoni et al., 2019)) are overlaid on the cortical surface. Abbreviations: M1 = primary motor cortex, PMd = dorsal premotor cortex, AG = angular gyrus, V1 = primary visual cortex, SPL = superior parietal lobule, FEF = frontal eye field, DLPFC = dorsolateral prefrontal cortex, LPC = lateral parietal cortex.

Conclusions: Stimulation dose likely impacts both behavioral outcomes and neural activity. While at the level of BOLD response, peripheral effects due to louder clicking and sensation might increase as a factor of stimulation intensity, behavior might change during specific intensities only. Nevertheless, side effects such as muscle twitches or disruption of attention due to stimulation sensations might also increase with increasing intensities which may result in unspecific behavioral effects as well (see Ref. [64]). To avoid under- or overstimulation, piloting might be helpful. Additionally, induced electrical field strengths might be aligned across participants as supported by electrical field simulations (e.g., Ref. [65,66]). It should be borne in mind, however, that BOLD responses due to increased loudness or somatosensation might blend in more strongly if stimulation intensity increases.

5.4. Stimulation frequency

The available studies suggest that stimulation frequency might modulate neural activity and behavior via specific entertainment. Hermiller et al. [32] compared entrainment effects of 2-s theta-bursts against beta frequency. Coupling between theta and gamma frequency (theta-burst) has been suggested to result in long term potentiation-like neuronal states [67,68]. The study by Hermiller et al. showed that hippocampal BOLD-changes (as obtained from region-of-interest analyses) and behavioral changes were specific for theta-burst stimulation.

Conclusions: To date, only one study systematically investigated the effect of entrainment on BOLD and behavior. This study indicated that a beta (12.5 Hz) TMS protocol does not result in any specific entrainment to the hippocampal system compared to patterned stimulation (gamma-theta coupling). In the disruption approaches discussed here, when stimulation is applied in the alpha-beta range, frequency does not appear to be a primary determinant of the behavioral outcome. This aligns with findings from a meta-analysis of online TMS studies [69]. Regarding the hemodynamic response, pulse frequency (i.e., 1, 4, 8 Hz) has been shown to influence activity in the cat visual cortex [70]. However, no study to date has compared activity modulation across different frequencies while simultaneously investigating cognitive processing and BOLD responses in humans. This highlights the need for further research.

5.5. Peripheral effects

Aside from transcranial effects, TMS also evokes non-transcranial effects, which might influence the BOLD response and behavioral outcomes. These include 1. activation of primary auditory cortices (A1) due to the clicking noise evoked by fast electrical field change [62] and potentially beyond as a consequence of neuronal entrainment [71], 2. activations of brain areas associated with somatosensation, including primary somatosensory cortex (S1), motor cortex (M1) and insular cortex, and 3) switches in attention as a result of the latter effects.

To avoid confounding effects in the context of interleaved TMS-fMRI during specific tasks, different control approaches have been chosen (Fig. 3). These include: 1. stimulation intensity: the application of low-

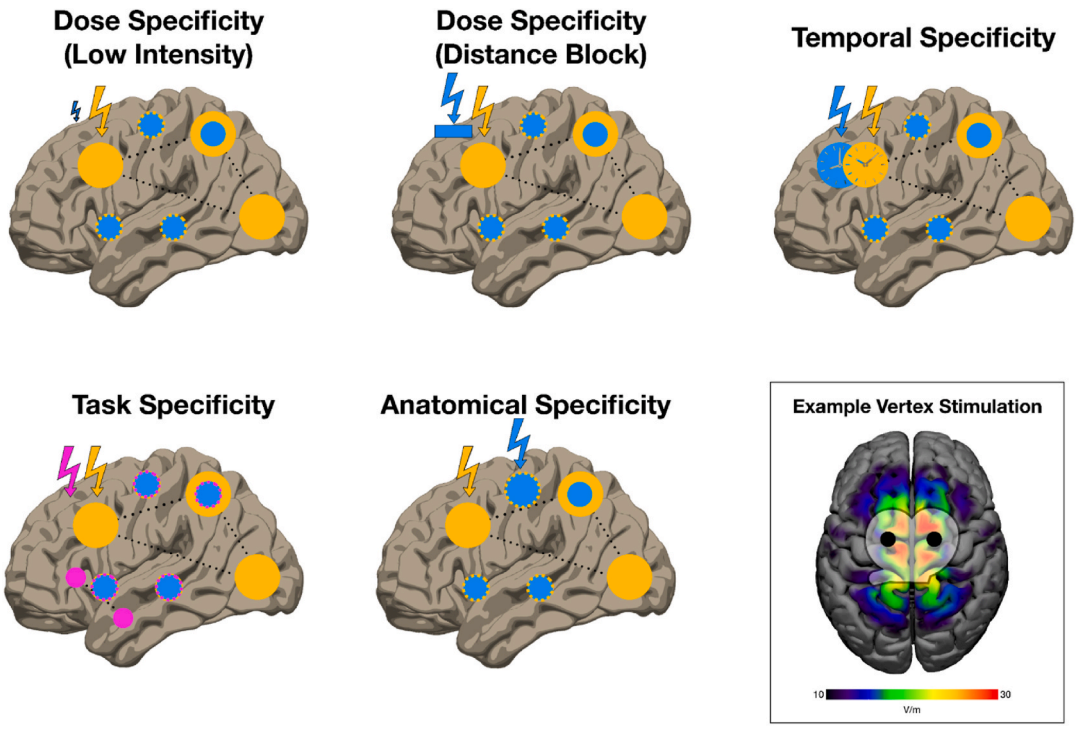


Fig. 3. Overview of control conditions and example electrical field simulation for vertex stimulation. Different approaches may account for non-specific TMS effects: Dose Specificity: stimulating at low intensities as control (top left), or using a distance plate (top middle). Temporal specificity: stimulating at different onsets relative to the task. Task specificity: stimulation during a control condition (illustrated in pink) engaging different cortical areas. This might result in activation increase in areas that are responding to non-transcranial effects (blue) for both conditions thus subtracting each other. Anatomical Specificity: stimulation of a different area (that is not part of the network of interest). Blue circles illustrate areas associated with peripheral TMS effects.
Lower right: E-field (magnitude) for a typical vertex stimulation using the Cz electrode position as reference (coil orientation: along the longitudinal fissure, cable posterior; coil model: MagVenture MRi-B91) and an arbitrary current change rate of 45 di/dt. Peak E-field is in the primary motor cortex and supplementary motor area.

intensity pulses (mostly around 40 % relative to the MT), 2. sham stimulation (distance block): increasing the distance between TMS coil and cortex while maintaining the same intensity by means of introducing a rigid body between coil and cortex, 3. stimulation timing: stimulating at different times relative to the stimulus onset, 4. control conditions: stimulation during different tasks and 5. control site (active stimulation): stimulating at different sites. To date, no commercially available sham-coil is compatible with the MR environment.

While method 1, 2 and 5 are theoretically also feasible during task-free TMS-fMRI experiments, option 3 and 4 are specific to experiments that involve a task. In the following, the application of these control strategies in the reviewed studies are discussed with regard to their potential influence on BOLD and behavioral effects. A short overview on advantages and disadvantages of the procedures can be found in Supplementary Table 1.

Low intensity pulses & distance block (dose specificity). The use of low-intensity pulses is supposed to mimic auditory and somatosensory effects of TMS without inducing any direct cortical effects. The advantage of this approach is that it allows one to deliver pulses at different intensities within one run of the same task. A potential issue is that the induced peripheral effects might not be of the same intensity as compared to the intensities applied during cortical stimulation. This is because of lower clicking noise and sensory effects (e.g. muscle twitches, scalp pain, feeling of vibration) induced by lower intensities. This approach is applied frequently in the studies reviewed here [18–20,23,26,27,30,35–37]. While most of these studies suggested that this method is appropriate to investigate specific TMS effects, some study results indicate that non-transcranial effects might be reflected in neural activity change and blend with transcranial changes in activity for above threshold stimulation intensities. Low intensity stimulation might be perceived differently by participants as reflected in less pronounced changes in BOLD response in auditory and somatosensory regions. Therefore, interpretation of specific contrasts between above threshold and low intensity stimulation should always be done with this consideration in mind. The distance block follows a similar principle as the low intensity pulses avoiding induction of effective electromagnetic fields in the cortex, while maintaining the same stimulation intensity as in the effective condition. One downside of this approach is that real and sham stimulation cannot be performed within the same experimental run. Here, scalp-cortex distances might also be considered before stimulation to avoid effective stimulation in the cortex. Even though there is an exponential decline in the induced magnetic field as a factor of distance [72,73], some studies have found TMS effects with low doses [74,75]. This warrants further research on the effective stimulation dose induced to evoke an effect especially in association cortices [76]. Until now, only one study combining BOLD and behavioral effects reported a non-significant interaction between task and sham effects [24]. The main effect for real vs. sham stimulation revealed increased activation in the right superior parietal lobe, right postcentral gyrus and right paracentral lobule, potentially indicating non-transcranial effects.

Both strategies might additionally result in stimulation of cranial nerves that in turn might impact both BOLD response and behavior and warrant additional caution [77].

Varying stimulation onsets (temporal specificity). While stimulation before stimulus onsets has been associated with enhanced performance due to priming effects, the disruption of cognitive processes requires exact timing. Thus, stimulation with stimulus onsets might interfere with primary (visual or auditory) processing but not with the cognitive process of interest (see above for a discussion on timing effects). The advantages of this approach are that variations are possible within one

run, exactly the same spot is stimulated, and stimulation parameters are similar aside from the onset relative to the stimulus. Three studies so far have looked into timing effects during stimulation [27,31,34]. All of them found changes in BOLD response as a factor of timing and specificity of behavioral changes.

Control conditions (task specificity). fMRI experiments usually include a control condition for unwanted effects such as primary visual task processing. This control condition is supposed to not engage the stimulated area the same way as the task condition does. Stimulating during a control condition is similar to the different site condition (see below), but without having to move the TMS coil. In most existing interleaved TMS-fMRI studies, these effects were not evaluated separately, but in interaction with other control conditions (different intensities). However, applying TMS during a control task contributes largely to the specificity of the stimulation site in interaction with the cognitive process of interest, thus revealing task or process specificity.

Stimulating at different sites (anatomical specificity). Another possibility is to stimulate a different area. This has the disadvantage of requiring another stimulation session and different stimulation sites may result in different somatosensory and auditory side effects. However, an active control site allows evaluating the specificity of certain network nodes in terms of task involvement – if stimulating a different network leads to the same behavioral effects, this might indicate that the effect is due to non-specific TMS effects. In some studies, vertex stimulation is used as a control site. However, one interleaved TMS-fMRI experiment demonstrated that vertex stimulation leads to considerable network effects, especially activity decrease in the default mode network [78]. This is not surprising since conventional vertex stimulation results in stimulation of the supplementary motor area and adjacent premotor cortex. Beyond potential transcranial effects, deactivation in the default mode network might, however, also have been influenced by peripheral effects such as switches in alertness and sensory stimulation. An example simulation of an electrical field for typical vertex stimulation is provided in Fig. 3.

Conclusions: In the previous studies, researchers either used one or a combination of different approaches accounting for non-transcranial TMS effects [79]. Considering the heterogeneity of studies, no final conclusion can be drawn on the best approach to account for peripheral influences on BOLD and behavior. Overall, some studies suggest that TMS results in BOLD changes in brain areas that might be associated with primary auditory processing, shifts in attention and somatosensory processing. There is no clear evidence on how these effects affect the interaction between BOLD and behavioral response, requiring more systematic research. For future reference, it might be useful if authors would report results for all control condition comparisons separately for the community to evaluate the advantages and disadvantages of the different procedures. Furthermore, the efficacy of the blinding procedure should be evaluated after each experimental session using standardized questionnaires [80]. Finally, we wish to emphasize that the choice of the specific control condition also depends on the research question and the conclusions to be drawn from a particular study. In terms of experimental rigor, it is generally advisable to include adequate control conditions to guarantee specificity of all effects-of-interest in the specific study (see Ref. [64]).

5.6. Re-afferent feedback loops

Another potential issue during interleaved TMS-fMRI experiments is the influence of re-afferent processes evoked by the stimulation that in turn might affect the BOLD response. In this respect, it was discussed that motor effects evoked by M1 stimulation result in BOLD responses as a feedback mechanism ([15]; see also [10]). Considering more complex behavior might elucidate the relationship between BOLD and behavior and their interaction, since neural activity change should go beyond simple re-afferent feedback in primary sensorimotor or visual systems. For example, the amputee study by Bestmann et al. [35], provides evidence that not all BOLD response is due to re-afferent processes, since it was based on the participant's sensation of hand-movement in the absence of an actual hand. In their later studies [36,37], these authors designed a motor task that was not sensitive to TMS-induced modulation at the behavioral level to explicitly rule out BOLD changes due to behavioral effects and were still able to find BOLD modulations during task performance.

Similar to motor studies, it was also discussed if BOLD responses during V1 stimulation might arise from the perception of the visual phenomenon itself. However, the evidence for phosphene perception resulting in BOLD changes is weak so far [81]. In some interleaved TMS-fMRI studies investigating visual attention, the frontal eye field (FEF) was stimulated. The FEF is associated with saccade movement and stimulating FEF during visuospatial tasks interferes with saccadic preparation [82], potentially resulting in re-afferent feedback. In one interleaved TMS-fMRI study, the FEF was stimulated during a selective attention task focussing either on stimulus direction (cloud of arrows) or sex (based on facial features) as opposed to passive viewing of stimuli [20]. The authors found an increase in bilateral FEF activity during TMS for the active conditions. However, based on eye tracking data, there was no significant difference in saccades, which does not support a re-afferent influence during FEF stimulation. Accordingly, the studies by Ruff and colleagues (2006, 2009; [5,29]) did not indicate any obvious effects of FEF stimulation on eye-movements (see Supplementary Information).

During other cognitive tasks not directly targeting the somatomotor or visuomotor system, on the other hand, stimulation improved or impaired task performance. In terms of interleaved TMS-fMRI studies, most protocols aimed for perturbation effects, while only some approaches observed improved task performance [19,31–33]. Thus, investigating task-specific changes in the BOLD response as a proxy of the underlying cognitive process is in these cases the exact focus of the study. Future studies might leverage the high temporal resolution of TMS to disentangle different stages of TMS effectiveness including feedback loops of cognitive processes [83].

5.7. Technical limitations

Overall evidence on BOLD-behavior interactions warrant some additional caution considering some technical limitations of the interleaved TMS-fMRI protocols, especially limited brain coverage (reduced field-of-view; signal loss due to TMS coil placement between scalp and radio frequency (RF)-coil), signal-to-noise ratio and relatively long repetition times (TRs; $\geq$2 s; see Table 1 for details). Concerning limited brain coverage and signal-to-noise ratio, local stimulation effects might not have been detectable, biasing conclusions on local BOLD changes and limiting study results to region of interest analyses. Furthermore, long TRs that were introduced to allow for volume gaps to ensure artifact free stimulation might have missed task-specific BOLD responses, additionally limiting conclusions.

6. Conclusions

The above discussed interleaved TMS-fMRI experiments are heterogeneous in terms of design, task, stimulation protocol and statistical approaches. Stimulation frequency was mostly in the alpha to beta range, with the intention to induce a disruption of cognitive performance [59]. Factors that appear to most strongly influence study results on BOLD-behavior interactions include task demand and stimulation timing, as these are central to state-dependent stimulation effects – specifically, stronger TMS responses driven by brain state manipulation [50].

The most popular cognitive domain for interleaved TMS-fMRI studies to date is attention, and most experiments targeted the right hemisphere. The language domain has not been investigated so far (compare [84]).

Interestingly, cognitive enhancement effects were mainly reported

for memory tasks and linked to remote activation changes. This might not come as a surprise, considering the hippocampus as a core region for brain plasticity and memory formation. Noteworthy, one study was explicitly designed to address stimulation-induced changes in the hippocampus during memory encoding [32]. According to Luber & Lisanby [85], there are at least three mechanisms that could result in cognitive enhancement due to TMS: 1. enhancement effects in task-relevant cortex, 2. enhancement by indirect stimulation effects (disruption of processes that compete with targeted processes), and 3. enhancement by non-specific effects (e.g. intersensory facilitation [86]). Interleaved TMS-fMRI has the potential to address all three mechanisms and, with adequate control conditions, disentangle the contribution of these effects. While there is some evidence for remote effects [19,31–33], local effects of cognitive enhancement have not been uncovered so far. The above-discussed enhancement effects might be related to priming effects induced by TMS. Such effects warrant further investigation to unravel potential remote activation changes underlying this phenomenon [47].

Another relevant topic for future studies would be to disentangle the interaction between overall peripheral effects and transcranial TMS effects. Typical areas activated by peripheral TMS effects are opercular and somatomotor areas [62]. Some study results discussed here suggest such interactions [17,26,43,42]. The impact of stimulation timing has also been highlighted [27,31,34]. Consequently, prior piloting is advisable to obtain a first estimation of specific effects of interest [27].

To better understand why some TMS protocols result in remote and others in local activation changes, future studies should always report the following details: 1. univariate fMRI results including separate maps for all task conditions to enable activation likelihood-based meta-analyses and comparisons across larger samples, 2. correlation analyses for task performance and BOLD responses to guide interpretation of the functional relevance of the observed changes, and 3. potential network effects in remote, connected areas. Such effects might be elucidated with connectivity analyses at rest and during specific tasks. A promising approach to provide insight into state-dependent network effects would be to link individual stimulation-induced connectivity profiles at rest with those obtained during a task of interest (see Ref. [87] for a first approach with TMS before fMRI). Here, the use of sophisticated graph theoretical measures might help to better understand large-scale network effects.

CRediT authorship contribution statement

Anna-Lisa Schuler: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Gesa Hartwigsen:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors have no conflicting interests to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.brs.2024.12.1190.

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