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Approaches to map cortical excitability beyond the primary motor cortex – Perspectives from cognitive neuroscience, multimodal imaging and clinical applications

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ABSTRACT

Excitability is a neuronal property quantified as the magnitude of neural response to stimuli. It plays a crucial role in information processing and is disrupted in various neuropsychiatric conditions. In humans, non-invasive measurements of brain excitability have been mostly limited to the primary motor cortex. Here, the response to Transcranial Magnetic Stimulation (TMS) is quantified as the magnitude of the muscular contraction. TMS mapping of brain excitability outside the motor cortex, simultaneously across brain areas, and in deep regions is challenging. Indeed, TMS has little depth penetration, and can only probe one cortical point at a time. Furthermore, the measurement of the responses to stimuli outside the motor cortex requires simultaneous neuroimaging, such as electroencephalography (EEG) and functional magnetic resonance imaging (fMRI). Possible solutions include the application of stimulation approaches alternative to TMS, and the investigation of resting state properties of electromagnetic and hemodynamic brain activity. We show that, in combination with TMS or alone, neuroimaging will progressively allow non-invasive and accurate mapping of excitability with high spatio-temporal resolution, across the entire brain, and non-invasively. This will mark a critical advancement for stimulation thresholding in basic neuroscience and clinical medicine, as well as diagnostics of deviant excitability patterns in neuropsychiatric conditions. It is the aim of this review to critically discuss the state-of-the-art of whole brain excitability mapping and provide an outlook on neuroscience and clinical implications.

1. Introduction

1.1. The question of a definition and the challenges of TMS mapping

The concept and definition of cortical excitability are often treated elusive or controversially. From an operational perspective, cortical excitability refers to the neurophysiological property that encompasses the reactivity of cortical neurons to given stimuli. Based on an interplay between neuron reactivity and response specificity, this property is fine-tuned in time and across brain areas and thus allows information integration and ultimately efficient brain function (Ly et al., 2016). At the core of cortical excitability is the balance between excitation and inhibition in neuronal circuits that is regulated by excitatory glutamatergic and inhibitory GABAergic neurons (see chapter below). On a large-scale neural network level, it is furthermore governed by the interplay of cortical and subcortical network hubs (Biswal et al., 2010; Dubbioso et al., 2022). Finally, cortical excitability is modulated by the input of sensory organs and motor outputs, as well as the current vigilance state of the individuum including circadian rhythm (Meisel et al., 2015; Ly et al., 2016). Excitability is impaired in nearly all neuropsychiatric conditions, especially, epilepsy, migraine, stroke, ADHD etc. (Badawy et al., 2013; Di Pino et al., 2014). In standard practice, cortical excitability is measured by applying standardized stimuli and quantifying elicited responses (Rossini et al., 2015). For example, the muscular

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contraction resulting from stimulation of the primary motor cortex is the proxy to measure corticospinal excitability (Raffin et al., 2015; Di Lazzaro et al., 2004). In humans, Transcranial Magnetic Stimulation (TMS) is the gold standard non-invasive stimulation approach to assess cortical excitability. TMS generates brief and intense electromagnetic pulses, which result in electrical currents in the cerebral cortex, and depolarization of neurons (Barker, 1991; Siebner et al., 2022). Although TMS is a powerful technique, it has severe inherent limitations. Indeed: a) it can usually be delivered at one site at a time, resulting in sparse spatial and temporal sampling; b) it does not directly reach deep regions, limiting the spatial coverage; c) it might interact with excitability (rather than testing its ongoing state).

A variety of additional brain specific issues arise with the application of TMS to estimate cortical excitability, including: 1. brain areas have different cytoarchitectonic features, which influence their susceptibility to external stimuli (here TMS, (Turi et al., 2022)), 2. cortical areas differ strongly in their remote connectivity patterns to other functional hubs of the targeted neural network (Biswal et al., 2010; Schuler et al., 2019), 3. intrinsic excitability fluctuations might differ strongly over different cortical regions (Dugué et al., 2011; Gal et al., 2010; Johnson et al., 2012), 4. brain disorders often affect multiple large brain networks, so that estimating excitability from one region is inevitably associated with information loss (Cortese et al., 2021). Moreover, measuring the response to TMS in brain regions where observable change in behavior is hard to detect poses an additional obstacle. For example, the stimulation of associative cortices, such as the parietal cortex or the dorsolateral prefrontal cortex do not have an established recognizable behavioral readout. In these cases, TMS can be combined with simultaneous neuroimaging, for instance electroencephalography (TMS-EEG; Gogulski et al., 2023; Raffin et al., 2020; Kähkönen et al., 2005; Lioumis et al., 2009) or functional magnetic resonance imaging (TMS-fMRI; Tik et al., 2023a,b; Webler et al., 2020; Li et al., 2004; Deng et al., 2022). Both methodologies are challenging (Bergmann et al., 2016; Conde et al., 2019; Pellegrino et al., 2022), technically demanding, prone to artifacts, and require advanced skills from the operators.

It is the aim of this review to critically discuss different methods to evaluate cortical excitability beyond primary motor cortex and their future implications for basic research and clinical medicine. Advancements in these methodologies might provide critical information on stimulation thresholding procedures and diagnostics on excitability deviations and their treatment in the future.

1.2. Inhibition/excitation circuits at the core of excitability measures

A property tightly linked to excitability is the excitation/inhibition balance (E/I). E/I refers to the equilibrium between excitatory and inhibitory activity in neural circuits. It depends on the ongoing fluctuations of synaptic inputs and regulates the generation of field potentials (Gao et al., 2017). Multiple E/I components contribute to defining cortical excitability as assessed by stimulating the brain with TMS. In essence, single pulse TMS assesses excitability by interacting with neurons spanning across all cortical layers, yielding a response shaped by both excitatory and inhibitory interneurons. Limited to the motor cortex, at one point, at one time, specific TMS paradigms (paired pulse TMS, afferent inhibition, etc.) can be exploited to estimate E/I, and to demonstrate that higher E/I corresponds to higher excitability (Lazzaro and Ziemann 2013). Recent evidence, however, suggests the possibility of assessing E/I by exploiting various features of electromagnetic and hemodynamic resting state signals. These signals can be easily and non-invasively measured with EEG or magnetoencephalography (MEG; Ahmad et al., 2022; Donoghue et al., 2020; Pellegrino et al., 2020a; Pellegrino et al., 2023) and fMRI or functional near-infrared spectroscopy (fNIRS; Cai et al., 2022; Trakoshis et al., 2020). While the relationship among various E/I estimates, intracortical circuits, and excitability remains to be understood (Pellegrino et al., 2023), a new framework, centered on the significance of resting state data in informing about E/I, holds the potential to trigger a significant paradigm shift. This framework would indeed enable the assessment of excitability with high spatial and temporal resolution, extensive brain coverage, and non-invasively (Fig. 1 (all figures created in BioRender.com); Ahmad et al., 2022; Di Lazzaro and Ziemann, 2013; Larsen et al., 2018; Pellegrino et al., 2019a).

How brain properties are linked to each other, and how one property could be inferred from the others is a fundamental field of investigation. Here, we discuss the relevance and the possibility to infer excitability from other neurophysiology and neuroimaging data, in combination or independently from TMS.

1.3. TMS and mapping of the primary motor cortex

Excitability has been mostly assessed in the motor cortex in humans. This region is superficial and easily accessible to TMS to deliver standardized stimuli. The motor cortex is connected to peripheral muscles by a chain of two neurons, which makes the response to stimuli easy to measure with superficial electromyogram (EMG) as muscular contraction (Rossini et al., 2015). Excitability can be expressed in several ways, including resting motor threshold resting (rMT), active motor threshold (aMT), and amplitude of the motor evoked potential (MEP). The rMT is the intensity of the stimulation at which half of the stimuli elicit a 50 microvolts response in the target muscle at rest, while the aMT follows the same concept but with the preinnervation of the corresponding muscle. Active motor threshold has been somewhat overlooked, likely because it is influenced by the level of active muscular contraction, which is difficult to accurately control in some settings. Motor cortex excitability increases with motor imagery and motor activity (Hallett, 2007), therefore the aMT is lower than the rMT. aMT has been mostly used to identify the stimulation intensity for rTMS protocols, including theta burst stimulation. Lower motor thresholds correspond to higher excitability. The amplitude of the MEPs is measured from peak to peak (negative and positive deflection; Rossini et al., 2015). Typical MEP amplitudes range between 50 microvolts up to a few millivolts before the amplitudes saturate (Kukke et al., 2014). Each peripheral muscle has its own specific excitability (Kallioniemi et al., 2014), although neighbouring muscle groups, i.e., hand, leg, and face, commonly have similar excitability levels (Fig. 2; Sondergaard et al., 2021). To compare MEP amplitudes (and excitability) across people, the stimulation needs to be standardized across individuals. The same stimulation intensity, however, results in a different 'dose' at cortical level due to anatomical and excitability variability across individuals (Säisänen et al., 2008). To overcome this, the TMS stimulator output is normalized to the individual MT (for example TMS intensity is set at 120 % of the MT). Several approaches exist to estimate the MT, such as the Rossini-Rothwell (Rossini et al., 2015), Mills-Nithi (Mills and Nithi, 1997), and threshold hunting (Awiszus, 2003). Although the methodology underlying these approaches is slightly different, they all estimate the MT as a stimulation intensity that evokes MEPs of at least 50 microvolts in 50 % of the times a single TMS pulse is applied (Rossini et al., 2015) and provide similar results (Tranulis et al., 2006). Thus, by definition, the MT is not supposed to evoke an MEP at every stimulation accounting for excitability fluctuations in the targeted cortex. All MT estimation methods require several TMS pulses to be applied before the threshold is reliably obtained. This is because the MEP amplitude is highly variable between consecutive MEPs (Kiers et al., 1993). Investigations on motor mu oscillatory phase could differentiate low and high excitability states of the motor cortex (Bigoni et al., 2024; Zrenner and Ziemann, 2023; Zrenner et al., 2022; Tabarelli et al., 2022; Karabanov et al., 2021). Nevertheless, if the state of the individual does not change, the MT is a relatively stable measure (Danner et al., 2008; Engelhardt et al., 2019; Kimiskidis et al., 2004; Sankarasubramanian et al., 2015; Ter Braack et al., 2019). The MEP is measured from a peripheral muscle, and the characteristics of the spinal motor neuron as well as neuromuscular junction and muscle contribute to its amplitude. Thus, motor cortex TMS

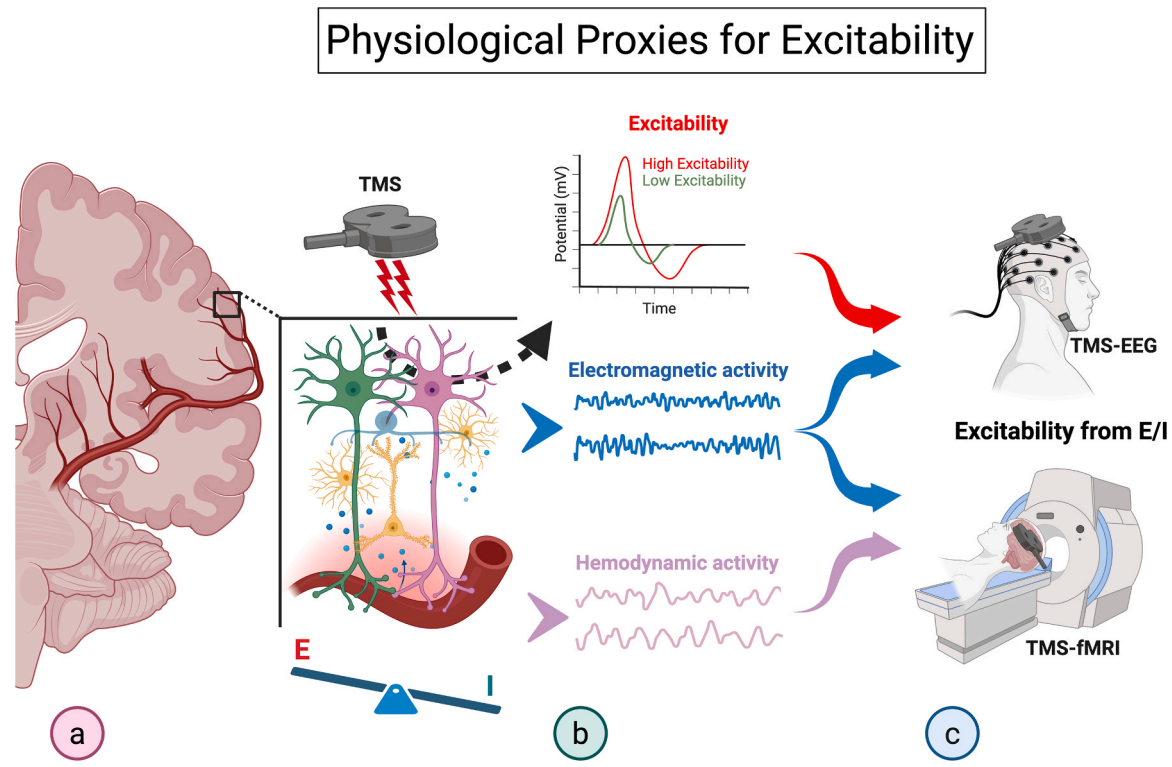


Fig. 1. Relationship between different Measures underlying Excitability. Excitability, Excitation-Inhibition (E/I) balance, Electromagnetic activity and Hemodynamic activity are cortical properties linked to each-other (panel a & b). Each of these properties are assessed by different neurophysiology and neuroimaging tools, with TMS establishing itself as the tool of choice for excitability (panel a), EEG and MEG for the measurement of electromagnetic activity, and fMRI and fNIRS as the tools to measure hemodynamic activity (panel c).

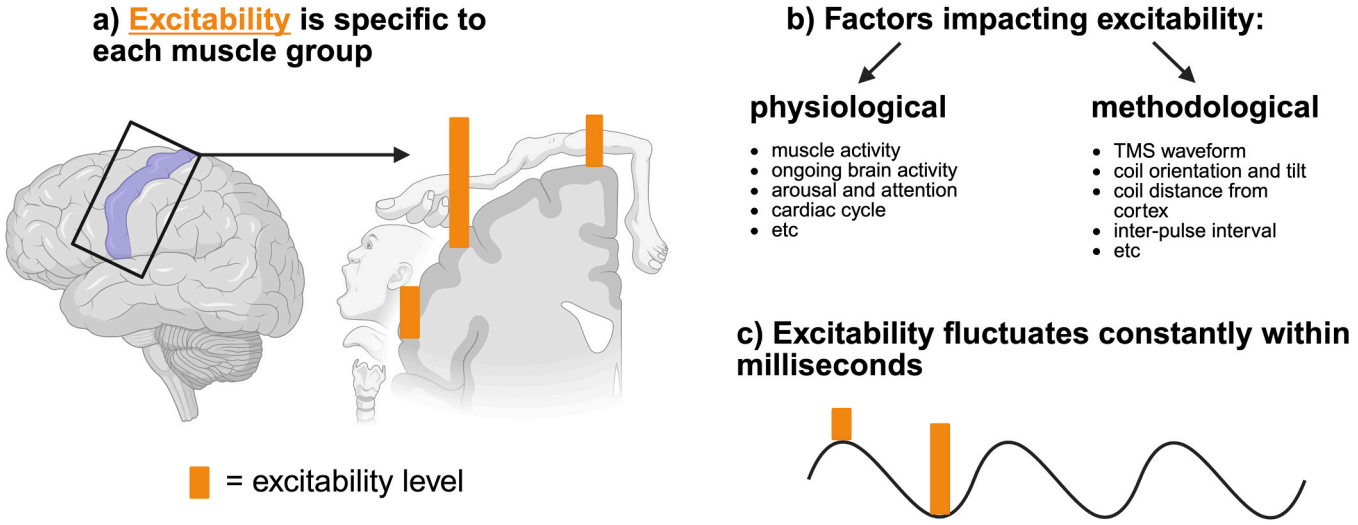


Fig. 2. Specificity of Motor Cortex Excitability. *Panel a)* Excitability in the motor cortex is specific to each muscle group. Typically, the hand area is the most excitable, i.e., the smallest motor threshold, compared to the leg and face area. *Panel b)* Several physiological and methodological factors impact the measured excitability and *Panel c)* excitability fluctuates constantly.

provides a measure of corticospinal excitability or excitability of the motor system rather than a purely cortical measure. A number of factors influence motor excitability (Fig. 2), including but not limited to, the level of background muscle activity (Wassermann et al., 1996), the arousal and attentional state of the study participant (Gandevia and Rothwell, 1987), the ongoing brain activity (Ferreri et al., 2014), cardiac cycle (Al et al., 2023), as well as methodological factors, such as the applied TMS waveform (Lynch et al., 2022), TMS coil orientation (Kallioniemi et al., 2015; Raffin et al., 2015) and tilt (Rossini et al., 2015), and the distance between the TMS coil and the cortex (McConnell et al., 2003; Stokes et al., 2007). Additionally, when MEPs are repeated, the metabolic state of the target muscle could have an impact (Kallioniemi et al., 2019), and if the applied inter-pulse interval is too short, cumulative effects could also occur (Fig. 2; Julkunen et al., 2012; Kallioniemi et al., 2022a; Pellicciari et al., 2016). Therefore, stimuli should be delivered with a jittered inter-stimulus interval of several seconds. The spatial sampling is limited to a few points that are being tested. This is a strong limitation given the ongoing remapping of

cortical excitability, such as in the primary motor cortex (M1; Raffin et al., 2015; Vasileiadi et al., 2023). Multichannel TMS coils, robotized or manual stimulation combined with predictive algorithms might overcome this limitation in the future (Harquel et al., 2017; Meincke et al., 2016; Tervo et al., 2020; Tugin et al., 2021; Souza et al., 2025).

The motor cortex has been the main target for the study of cortical excitability since the early eighties of the last century. While MT and MEP amplitude from single pulse TMS provide information on the excitability of the cortex as a whole, starting in the nineties the development of protocols, such as paired pulse TMS, silent period (SP; Fuhr et al., 1991), combined peripheral and central TMS stimulation have allowed a careful characterization of intracortical circuits, up to identifying the state of inhibitory and excitatory components contributing to the E/I balance. As a marker for inhibition, the SP reflects the activity of the GABAergic system (Daskalakis et al., 2007). The SP has large between-subject variability which is mitigated by using individualized SP thresholds (Kallioniemi et al., 2014). SP, however, is not as widely applied as the MEP (Roick et al., 1993). Other TMS protocols exist to characterize the excitability and connections of the primary motor cortices, such as dual coil TMS, ipsilateral silent period, short-interval intracortical inhibition (SICI), intracortical facilitation (ICF), short-latency afferent inhibition (SAI), long-latency afferent inhibition (LAI), etc. The reader is referred to (Rossini et al., 2015; Kallioniemi and Daskalakis, 2022) for a comprehensive discussion of these approaches.

1.4. Beyond M1

While the motor system—particularly the corticospinal response of hand muscles to TMS pulses—is considered the gold standard for assessing excitability, these excitability measures are not as straightforward as often perceived from a purely mechanistic perspective. Readouts beyond the primary motor system have been rarely addressed, since they add some extra challenges, such as defining the proper readout (in behavioral experiments) or combining TMS with additional imaging or neurophysiological techniques (Fig. 3). A further obstacle is that brain areas beyond M1 are mostly embedded in more complex functional network structures, which makes it even harder to evaluate cortical responses to a spatially circumscribed TMS pulse. In the following sections we will discuss literature on the measurement and mapping of cortical excitability and provide conclusions for future research.

Specifically, we will discuss extrinsic measures of excitability beyond M1 that rely on the combination of TMS with readouts such as, behavioural, EEG or fMRI responses. Moreover, we will discuss intrinsic measures of excitability, i.e., specific analyses of resting state M/EEG or fMRI data without any external brain stimulation. Since these measures do not rely on any external stimulation, they were termed intrinsic measures and are supposed to represent intrinsic neural fluctuations rather than the reaction to an external stimulus (Meisel et al., 2015). An overview on main measures discussed here is found in Fig. 3.

Literature was considered from inception to March 23rd, 2025, and was searched via PubMed and Google Scholar. Criteria of inclusion were the description of measures of excitability combining behavioural, oscillatory and hemodynamics with TMS in a dose dependent manner. For completeness we have added additional sections on fNIRS, other stimulation approaches (peripheral, invasive) and intrinsic measures of excitability that are based on resting state M/EEG and hemodynamic data.

1.5. TMS and behavioral measures

Similar to M1, threshold-hunting methods have been applied to other cortical regions, as long as they are accessible via TMS and linked to a measurable behavioral readout. Thus far, this approach has been primarily limited to the visual domain (Fig. 4), where the most common response and excitability measure is the phosphene threshold (PT). Phosphenes are flashes of light that can be perceived by a person due to TMS stimulation of the primary visual cortex (V1) or interconnected

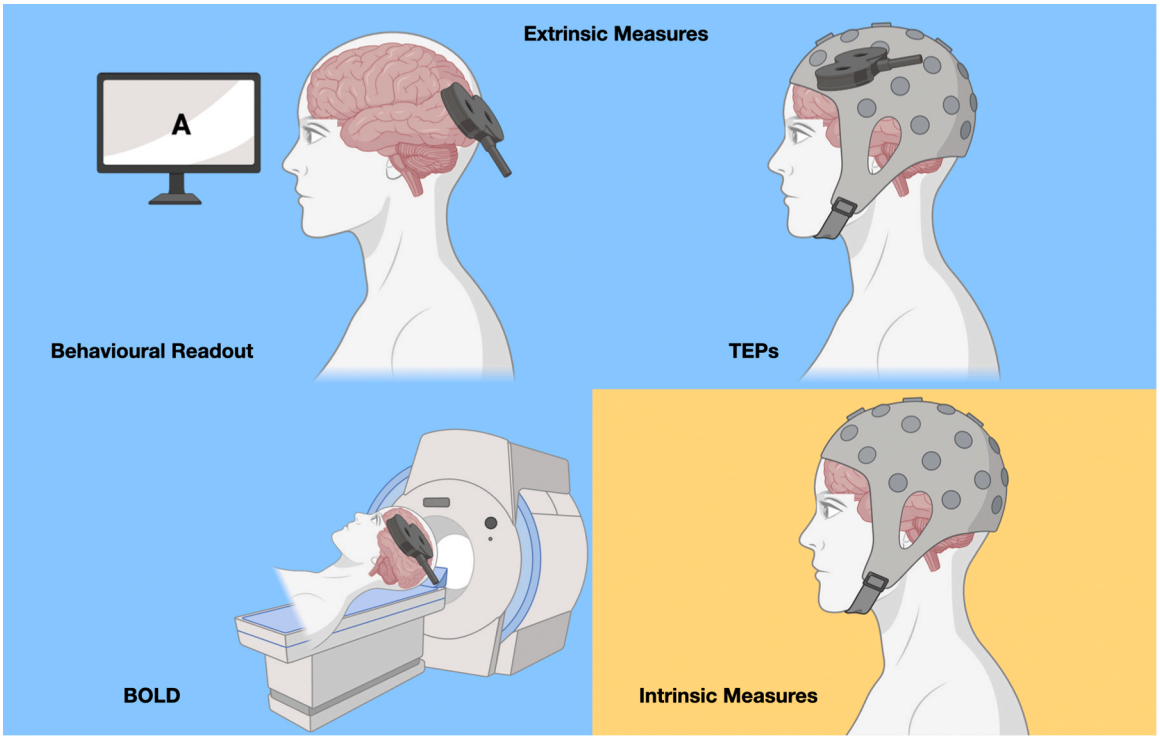


Fig. 3. Main Methods to be discussed in this Review. Cortical excitability beyond M1 has been approached with a variety of measures, such as TMS in combination with behavioral readouts. Other studies combined TMS with EEG or fMRI/fNIRS in order to evaluate cortical excitability. More recent approaches focus on intrinsic measures derived from ongoing neural oscillation patterns or BOLD fluctuations (intrinsic measures).

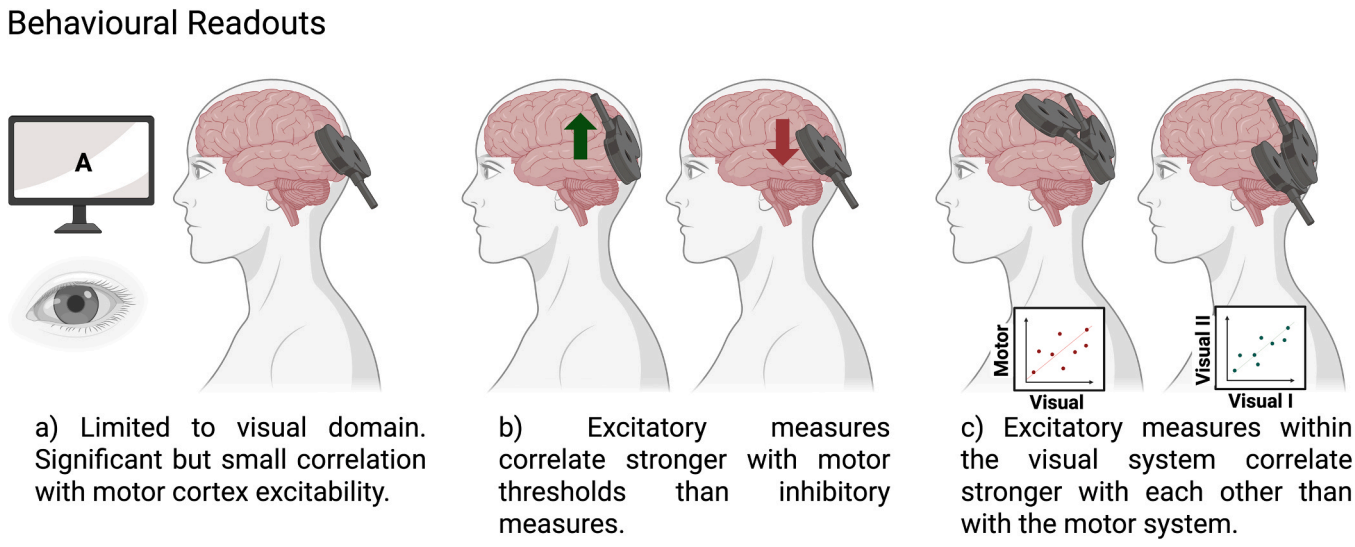


Fig. 4. Behavioural Measures as Readout for Cortical Excitability. *Panel a)* Cortical excitability using a combination of TMS and behavioral readouts have been limited to the visual system (phosphenes, moving phosphenes and interference with visual stimulus processing). *Panel b)* Effects of excitatory measures such PT are stronger related to MT as compared to inhibitory measures, such as task interference. *Panel c)* Excitatory measures seem to be cortex and domain specific.

areas (V3/V5, posterior parietal cortex; for a review see (Turi et al., 2021)). Some authors have, however, explored the possibilities of inhibitory measures during task performance (Oliver et al., 2009; Siniatchkin et al., 2011). Studies examining the relationship between V1 and M1 thresholds have produced conflicting results, likely due to the fact that excitability is finely modulated across time and space. The patterns of excitability vary between regions, reflecting differences in structure, cytoarchitecture, and function (Antal et al., 2004; Boroojerdi, 2002; Deblieck et al., 2008; Gerwig et al., 2003; Stewart et al., 2001; Stokes et al., 2013). Indeed, Antal et al. (2004) showed a relationship between static and moving PT but not MT. Later studies (Deblieck et al., 2008; Stokes et al., 2007, 2013) have highlighted a certain degree of relationship across excitability patterns of distant regions (motor and visual), as summarized in a recent meta-analysis (Phylactou et al., 2024). However, effect sizes were small, suggesting that MT and PT are not directly transferable to each other. PT has had some clinical application for V1 excitability assessment in patients with migraine (Franca et al., 2006; Siniatchkin et al., 2009; Brückner and Kammer 2016a; 2016b), but it has not been widely integrated due to the relative difficulty in application. Turi et al. (2021) highlight that only a few studies used phosphene-based thresholds to adjust stimulation intensity in 30 years (Antal et al., 2004; Thut et al., 2005; Lang et al., 2007; Thompson et al., 2009; Fried et al., 2011; Caparelli et al., 2010; De Graaf et al., 2018). Threshold hunting of the visual cortex is even more challenging and less applied outside of V1. Moving phosphene assessment has rarely been applied to estimate the excitability in the V3/V5 area (Thompson et al., 2009; Battelli et al., 1999; Pascual-Leone and Walsh, 2001), and in the posterior parietal cortex (Fried et al., 2011). Interestingly, inhibitory measures do not always seem to relate as strongly to MTs as the excitatory PT (Fig. 4). This underlines that excitatory measures are more closely related to one another than to inhibitory measures. Two studies have approached the cortical excitability problem beyond M1 by evaluating the suppression/facilitation of visual task performance (Oliver et al., 2009; Siniatchkin et al., 2011). Oliver et al. (2009) stimulated the intraparietal sulcus while subjects had to perform a visuospatial task. They could show that the threshold to interfere with task performance was linearly correlated with the MT. On the other hand, Siniatchkin et al. (2011) stimulated V1 while participants were looking at letters, to evaluate inhibition of visual processing with low reliability.

1.6. TMS with EEG, fMRI and fNIRS

Are there alternative non-invasive methods to measure the response to stimulation outside the motor cortex? Stimulation induces various biological effects, which could be captured through neuroimaging modalities applied during the stimulation. The three neuroimaging modalities most commonly used in combination with TMS are electroencephalography (EEG), functional magnetic resonance imaging (fMRI), and functional near-infrared spectroscopy (fNIRS). In all cases, two conceptual challenges arise: first, defining the readout that reflects cortical excitability; second, standardizing the stimulation intensity (input-output curve discussed above). EEG provides measurements of electric brain activity generated by large populations of neurons. The effects of stimulation on electrical activity can be estimated in the time domain as TMS-evoked EEG potentials or TEPs (Pellegrino et al., 2016). Other effects can be found in the frequency domain, in the signal consistency across multiple stimuli and in connectivity patterns. Simultaneous TMS-EEG is a technically challenging modality (for a review see Hernandez-Pavon et al., 2023). As with other modalities, EEG responses to TMS stimulation are best characterized for the primary motor cortex. The TMS-evoked potential (TEP) consists of a series of positive and negative deflections, whose amplitude depends on the stimulation intensity (Saari et al., 2018), and which are believed to be associated with the activity of inhibitory GABAergic and excitatory glutamatergic systems, as well as interactions across brain networks, especially for later latencies (Kallioniemi et al., 2022b; Tremblay et al., 2019; Giambattistelli et al., 2014). Therefore, the very early local responses reflect local excitability (as early as a couple of milliseconds; Beck et al., 2024; Bertazzoli et al., 2025), whereas the later latencies most likely reflect the excitability and the connectivity of large cortical networks. The recent approach by Beck et al. (2024) involving the analysis of immediate TEPs recorded at high sampling rates within a 2 ms time window, might allow to disentangle the influence of different interneuron systems on excitability in the future.

The study of early TMS-elicited responses has only recently become feasible, thanks to advancements in simultaneous TMS-EEG acquisition technology and the development of high-sampling-rate EEG amplifiers. Until recently, global cortical excitability in TMS-EEG studies was estimated using the amplitude of the average signal across all recorded EEG electrodes, a measure known as the global mean field power (GMFP) of the TEP (Hernandez-Pavon et al., 2023). Similarly, global measures of excitability have been derived from other EEG domains, such as

frequency and phase consistency, by analyzing the event-related spectral perturbation (ERSP) and inter-trial coherence (ITC; Saari et al., 2018). The most consistent TEPs are observed in response to stimulation of M1, where they exhibit reproducible peaks (Lioumis et al., 2009). Nevertheless, like MEPs, several factors influence the variability of TEPs, including EEG equipment, acquisition parameters, data collection and preprocessing strategies (Bortoletto et al., 2015; Rostami et al., 2022; Bertazzoli et al., 2021), brain state (Guzmán López et al., 2022; Romei et al., 2008), cardiac activity (Al et al., 2023), fatigue (Otieno et al., 2019), sleep (Massimini et al., 2005), and initiation of motion (Nikulin et al., 2003). Also here, TMS is often delivered at intensities relative to the MT in order to compare differences in responses to increasing stimulation intensities (input-output relationships). In some cases, stimulation intensity is kept constant at a specific output and maintained at the lowest possible level to minimize stimulation artifacts and peripheral interference (Rocchi et al., 2021). There have been attempts to assess the TMS-EEG input-output curves across M1 and other brain areas which suggest different relationships, including linear (middle frontal gyrus) as well as exponential (M1) relationships (Kähkönen et al., 2005). This study, though a clear advance at the time, could not leverage the most recent technological development. Thus, GMFP used to rely on larger time windows with later time-points being especially sensitive to peripheral evoked potentials (PEPs). These PEPs might have contributed to the signal and be partly responsible for a linear increase in EEG response. Other, more recent, studies confirm an exponential relationship for M1 and suggest a plateau for DLPFC and superior occipital lobe (Fig. 5; Raffin et al., 2020). The latter effect might be due to methodological advancements that help to avoid PEPs in more recent TMS-EEG studies. These studies confirm that excitability varies not only across cortical regions but also follows specific input-output curves. Consequently, some authors have begun standardizing stimulation intensity based on the particular region under investigation (Koch et al., 2022).

TMS-EEG has been applied to map excitability outside of M1 during altered consciousness and pharmacological influence (Ferrarelli et al., 2010; Massimini et al., 2012; Sarasso et al., 2014; Ramakrishnan et al., 2019), in relation to different cytoarchitectural structures across brain areas Harquel et al. (2016), and focusing on specific aspects of the intracortical inhibitory-excitatory networks, applied for more complex TMS paradigms such as short-interval intracortical inhibition (SICI), long-interval intracortical inhibition (LICI) and intracortical facilitation (ICF; Cash et al., 2017; Lioumis et al., 2009). TMS-EEG remains however a difficult technique, in terms of dedicated equipment, artifacts from EEG stimulation, data analysis procedures etc. It is not widely available, not reliable enough and cost-effective to be applied for translational research so far.

Another option is to read the response to TMS stimulation in the hemodynamic activity measured with fMRI. This is the core principle of simultaneous TMS-fMRI (for a review see Mizutani-Tiebel et al. (2022); Fig. 6). As compared to TMS-EEG, TMS-fMRI has the advantage of investigating TMS effects of dose-response relationships also in deep brain regions remote from the stimulation site. There are three main drawbacks: 1) the need of an fMRI compatible TMS coil and the technology associated with this; 2) the poor temporal resolution of the fMRI BOLD signal; 3) BOLD responses are almost never seen after a single TMS pulse, but bursts of pulses are needed over a time period of at least 0.2 s.

Unfortunately, fMRI did not detect any TMS-related BOLD response from V1 stimulation (De Graaf et al., 2018), and inconsistent responses from DLPFC stimulation (Dowdle et al., 2018; Tik et al., 2023a,b; Li et al., 2004). This variability may be attributed to state and trait-dependent differences in individual excitability and need to be explored further (Grosshagauer et al., 2024; Tik et al., 2023b). Beyond local effects TMS-fMRI has been shown to be an effective tool for assessing downstream dose-response relationships (Tik et al., 2023a). Recently, it could also be applied to identify remote BOLD changes as a factor of stimulation intensity for whole iTBS protocols (Chang et al., 2024; Tik et al., 2025).

Similarly to fMRI, functional near-infrared spectroscopy (fNIRS) can track the cortical hemodynamic changes associated with TMS stimulation (Jöbsis, 1977; Scholkmann et al., 2014). By utilizing optical signals, fNIRS offers three key advantages when combined with TMS: 1) minimal interference and greater compatibility with TMS; 2) higher temporal resolution than fMRI; and 3) the ability to measure changes in both oxy-hemoglobin and deoxy-hemoglobin concentrations. The main drawbacks are that: 1) fNIRS optodes increase the distance between the TMS coil and cerebral cortex, thus requiring a higher stimulation intensity to achieve the same induced currents (e.g., motor and the

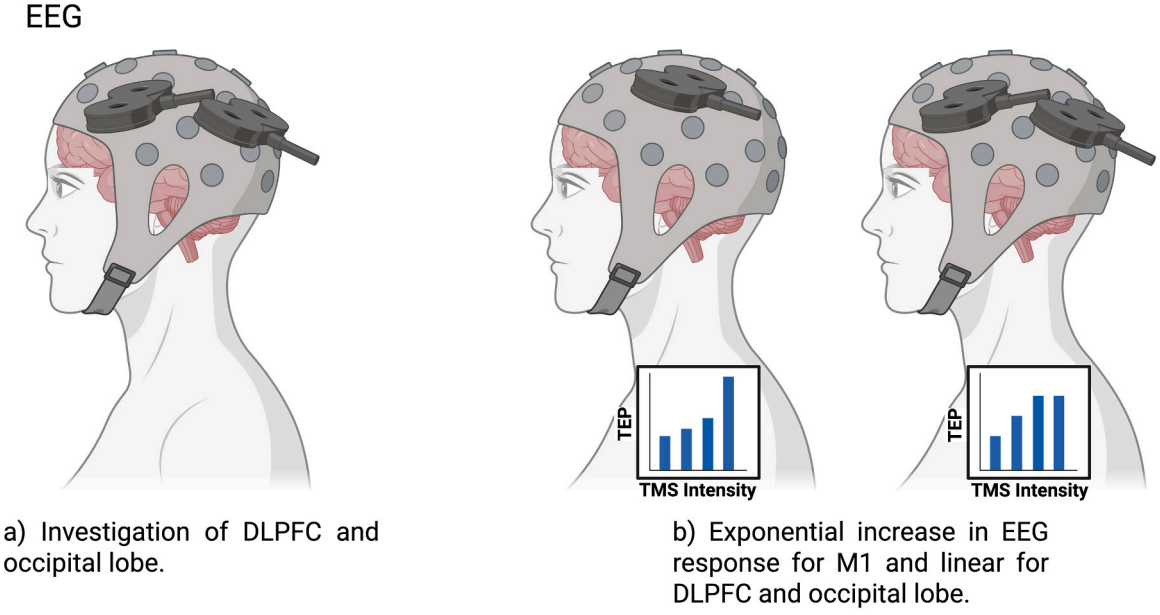


Fig. 5. EEG-based Input-Output Curve (Dose-Response Curve) across Cortical Regions. *Panel a)* TMS-based excitability with EEG has been probed in occipital cortex and DLPFC so far. *Panel b)* Excitability strength not only differs across cortical regions, but the relationship between stimulus intensity and response magnitude also varies. In particular, while the primary motor cortex (M1) follows an exponential relationship, the dorsolateral prefrontal cortex (DLPFC) and occipital lobe exhibit a linear relationship that plateaus at motor threshold intensity.

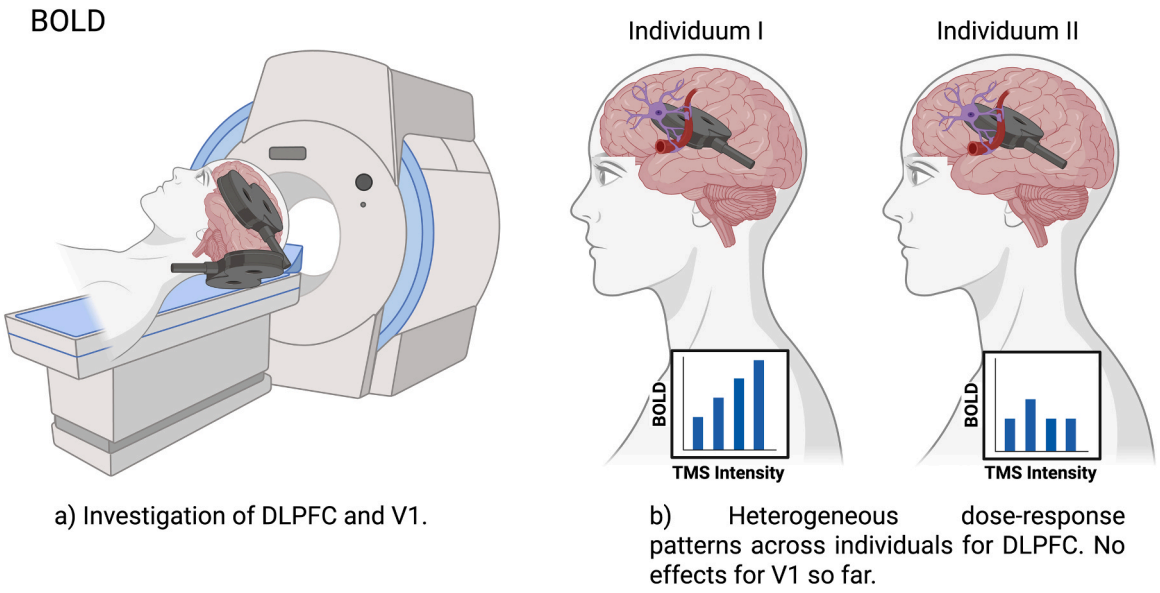


Fig. 6. TMS-fMRI to establish Dose-Response Relationships. *Panel a)* Relationship between BOLD and TMS intensity has been investigated in V1 and DLPFC. *Panel b)* So far, TMS-fMRI has failed to detect consistent excitability estimates as BOLD changes linked to TMS stimulation. The direct dose (stimulation) response pattern is highly variable across individuals requiring further research.

phosphene threshold are higher; Stokes et al., 2013); 2) fNIRS is particularly sensitive to the confounding of TMS-induced systemic circulatory changes (Mesquita et al., 2013; Cabrerizo et al., 2014; Mäki and Ilmoniemi, 2011; Näsi et al., 2011); 3) sensitivity to artifacts are linked to local scalp blood volume dynamic and local motion (Jasdzewski et al., 2003; Boden et al., 2007).

Increases in HbO were measured on the left M1 induced by single pulse (spTMS) at intensities of 90 %, 100 %, 110 %, 120 % and 140 % of the active motor threshold (Noguchi et al., 2003; Mochizuki et al., 2006; Furubayashi et al., 2013). Furubayashi et al. (2013) also reported decreases in HbR during rest at 120 % and 140 % active MT and smaller HbO increases when spTMS was delivered during voluntary contractions. Thomson et al. (2011) observed a significant decrease in HbO when spTMS was delivered at the left DLPFC at 130 % of resting MT. When compared to a lower intensity of 70 % resting MT, both spTMS and paired pulses (short interval intracortical inhibition and intracortical facilitation) demonstrated notable decreases in HbO at 120 % resting MT (Thomson et al., 2011). Curtin et al. (2019) on the other hand reported insubstantial hemodynamic responses induced by spTMS at 110 % resting MT. Conflicting observations between M1 and DLPFC stimulations may imply that spTMS-elicited hemodynamics are regionally specific. Note that except for filtering, none of these studies employed specific methodologies to remove systematic physiological noise, and local muscle and vessel contraction motion artifacts. Although there are some hints that fNIRS might be used to investigate cortical excitability, more research is needed to leverage this method for this purpose. Of note for an iTBS protocol over prefrontal cortex Zhang et al. (2022) found dose specific hemodynamic changes that also differed between men and women (Kan et al., 2024).

In summary, hemodynamics is a quite indirect measure for cortical excitability. Associations have been shown between hemodynamics and intrinsic neurophysiological measures of excitability (Hill et al., 2021) and there might be some relation between hemodynamics and TMS-evoked MEPs (Cai et al., 2022). Still the relationship between hemodynamics and brain excitability is complex and requires stronger validation in the future.

Finally, TMS coarsely stimulates excitation and inhibition systems, whose mechanisms are not picked up precisely with hemodynamics. Thus, hemodynamics might provide a better marker for network modulations than local TMS-effects of excitation and inhibition (Schuler and Hartwigsen, 2024; Woolgar et al., 2025). Based on the fact that hemodynamics reflect mixed effects from different cell types, changes in e.g. BOLD response as picked up as a consequence of TMS may not be attributed to excitation or inhibition systems in a straightforward manner (Mishra et al., 2021; Hall et al., 2016).

2. Other stimuli

Peripheral stimuli can be used as an alternative to TMS for studying neural excitability, particularly when combined with neuroimaging to record neural responses. This method is straightforward, with electrical stimulation of peripheral nerves being the most commonly employed technique (Dinse et al., 2023; Ranieri et al., 2022; Schabrun et al., 2012; Ohashi et al., 2019; Gorgoni et al., 2014; Litvak et al., 2007; Wolters et al., 2005; Wolter et al., 2013; Cruciani et al., 2024). Interestingly, certain stimuli can rapidly engage the entire cortical surface, particularly in the realm of auditory processing (Pellegrino et al., 2022; Pinardi et al., 2023). Auditory stimulation at 40 Hz entrains brain activity across the entire cortex (Wang et al., 2018; Schuler et al., 2022; Tada et al., 2021; Galambos et al., 1981) and provides access to specific intracortical circuits relevant to excitability, including GABA interneurons firing at 40 Hz (such as basket cells, parvalbumin positive cells), NMDA (glutamate) and GABA neurotransmission (Adaikkan and Tsai, 2020). Auditory-driven 40 Hz entrainment has been applied to detect excitability dysfunction in people at risk of schizophrenia (Larsen et al., 2018), in individuals with stroke (Pellegrino et al., 2019a) and in many other neuropsychiatric conditions (Deng et al., 2024). This approach has also been applied to map fluctuations of cortical excitability resulting from neuromodulation (Pellegrino et al., 2019b). These approaches typically provide limited spatial coverage (i.e. limited to primary cortices for somatosensory stimulation) and limited spatial resolution. They also have poor temporal resolution, as the measurement of the response to stimuli must be averaged across multiple stimuli to be detected with acceptable signal to noise ratio (Pellegrino et al., 2024). A particular case of alternative stimulation is the direct electrical stimulation of the cortex with invasive EEG (iEEG). This is common clinical practice in patients with drug-resistant epilepsy undergoing prolonged iEEG recordings. Similarly to TMS, the assessment of excitability can rely on a behavioral response (including triggering of epileptic seizures), or –as in TMS-EEG– in the iEEG response. In the latter case, response is

collected with the same iEEG electrodes used for the electrical stimulation. iEEG responses can be broadly classified as evoked (physiological response) and afterdischarges, which are the pathological clinical responses observed in the hyperexcitable cortical tissue of patients with epilepsy. In clinical practice, iEEG stimulation aims at inferring the location and extent of the epileptic region based on its responsiveness or excitability (Frauscher et al., 2023). The sampling is sparse, and the electrodes are placed in those brain regions supposedly relevant in the generation of epileptic seizures. Note that very recently, some groups have pioneered the hybrid combination of non-invasive stimulation with TMS and iEEG recordings. This research is obviously restricted to selected cases, but has the advantage of describing the electrical brain responses with unprecedented accuracy (Wang et al., 2024; Solomon et al., 2024).

2.1. Intrinsic measures

Here, we discuss the approaches aimed at extracting excitability without a controlled external stimulus, rather relying on properties of ongoing brain activity. Spontaneous fluctuations in neuronal activity are at the core of excitability fluctuations (Gao et al., 2017; Wang, 2020). Therefore, it has been postulated that excitability could be estimated by modeling resting state activity, both electromagnetically and hemodynamically. Various M/EEG metrics, including phase synchronization (Meisel et al., 2015; 2016; Schuler et al., 2023), the aperiodic component of the power spectrum (Gao et al., 2017), entropy (Liang et al., 2015; Wei et al., 2013), and alpha power (Pellegrino et al., 2021; Jensen and Mazaheri, 2010; Iemi et al., 2022), have all been linked to excitability. The recent advancements in M/EEG source imaging (Pellegrino et al., 2016; Pellegrino, Hedrich et al., 2018; 2020; Hedrich et al., 2017; Pellegrino, Maran et al., 2018; Pellegrino et al., 2020b; Afnan et al., 2023; von Ellenrieder et al., 2016) offer an intriguing opportunity to non-invasively map excitability at rest, providing full coverage of the neocortex, excellent temporal resolution and good spatial resolution. In this field, one of the most promising estimates comes from Meisel and collaborators and is based on the space phase synchrony in high gamma band (Meisel et al., 2015). This index was validated against gold standard excitability measurements with invasive EEG stimulation and recordings (Meisel et al., 2015), and against standard TMS recordings from M1 before and after experimental manipulation of cortical excitability (Pellegrino et al., 2023), ultimately gaining popularity for its versatility and ease of use (Schuler et al., 2023). Another interesting index is the exponent of the electromagnetic activity power spectral density, pioneered by Voytek's group (Donoghue et al., 2020; Gao et al., 2017). They demonstrated that the slope of the aperiodic PSD component (PSD minus the oscillation peaks) is linked to the E/I balance, with a lower exponent (less steep curve) corresponding to $E > I$. This measure has been validated in animal (Gao et al., 2017) and human models (Donoghue et al., 2020), has high spatial resolution, and good temporal resolution (Wilson et al., 2022). The availability of user-friendly toolboxes have favored its translation into the clinical world (Duma et al., 2024; Salvatici et al., 2024).

Nevertheless, this simple measure has its drawbacks: the estimation of the aperiodic component is not always accurate (Gerster et al., 2022), and the PSD is influenced by artifacts and noise. Simple oscillatory activity in alpha and beta bands have been often considered a mechanism and marker of inhibition (Jensen and Mazaheri, 2010; Hyvärinen et al., 2018; Pellegrino et al., 2021; Weisz et al., 2011; Frey et al., 2014; Wang et al., 2023). However, whether all alpha activity, its power, the phase, or bursts of alpha activity are all linked to inhibition or only some of these features is still a matter of debate (Madsen et al., 2019). Other metrics that have been related to excitability include entropy and indices extracted from fluctuation detrending analysis of the electromagnetic signals. Most likely, different measures capture complementary aspects of excitability and may display a different degree of correlation with traditional M1 excitability assessment based on TMS stimulation (Pellegrino et al., 2023). A more extensive review on intrinsic measures can be found here (Ahmad et al., 2022).

As previously mentioned, fMRI and fNIRS measure the hemodynamic activity, which depends on the concentration of oxy- and deoxy-hemoglobin, the metabolic demand, and blood supply. The modeling of hemodynamic activity to extract excitability thus includes further complex assumptions related to the relationship between fluctuations of electrical activity and fluctuations of hemodynamic activity, the so-called neurovascular coupling. Nevertheless, the intriguing aspect of this approach resides in the ability of fMRI to sample homogeneously the entire brain, with excellent spatial resolution. Several signal properties have demonstrated a link with excitability, including amplitude (Cai et al., 2022), regularity, predictability (Hurst exponent; Trakoshis et al., 2020), multiscale entropy (Kosciessa et al., 2020), amplitude of low-frequency fluctuations, and regional homogeneity (Zou et al., 2008; Zhang et al., 2010; Yang et al., 2022; Xue et al., 2017; Shi et al., 2021; Shi et al., 2024; Kosciessa et al., 2021; Muthukumaraswamy et al., 2009; Zhu et al., 2020; Zang et al., 2004). They do suffer from low temporal resolution, and have not been validated against TMS, but are gaining traction and becoming appealing for translational research (Xie et al., 2025; Xie et al., 2024; Bertelsen et al., 2023).

3. Conclusions and outlook

Excitability mapping beyond the motor cortex is fundamental to understanding brain physiology and could have vast, impactful clinical applications. Despite the use of TMS and other stimulation techniques in combination with neurophysiology and neuroimaging, this topic remains a significant challenge. Newly developed and tested intrinsic measures are likely to capture multifaceted aspects of brain excitability and the excitation/inhibition balance. Their use, either in isolation or in combination with brain stimulation, may finally make whole-cortex excitability assessment feasible and reliable, with high spatial and temporal resolution. Further studies are needed to standardize approaches and protocols and to accurately understand the biological significance of the different proposed methods and measures. Table 1 compares the main categories of measures investigated so far.

Taken together, the literature investigating TMS responses as a proxy for cortical excitability beyond M1 is relatively sparse. In terms of behavioral outputs, there have been studies successfully using TMS to investigate cortical excitability in visual regions. Most of them are based on subjects reporting phosphene perception (Stewart et al., 2001; Boroojerdi, 2002; Gerwig et al., 2003; Antal et al., 2004; Deblieck et al., 2008; Stokes et al., 2013). Others have used task performance as readout for stimulation intensity response, however, with mixed results on

Table 1
Comparison of main measures for excitability beyond M1.

	Potential Confounders	Group Level Results
Behavioural Readout	· Difficult to measure: - Phosphenes subjective - Other measures require well-selected tasks	Partially, individual needs to be preselected for phosphene thresholds; inhibitory measures require more research
TMS-EEG	· Requires specific hardware, typically a DC amplifier and TMS-compatible EEG caps · Artifacts from stimulation and peripheral TMS-effects · Requires expert operator	Evidence for group-level effects
TMS-fMRI	· Requires specific and expensive hardware, and advanced setup · BOLD is a more indirect proxy for excitability	No consistent group-level evidence at stimulation sites
Intrinsic Measures	· Heterogeneous validation strategies · No definite measure, so far	Evidence for group-level results

reliability (Oliver et al., 2009; Siniatchkin et al., 2011). Furthermore, no interleaved TMS-fMRI study has managed to show the neural correlates of phosphenes in an input-output fashion, questioning the capacity of BOLD response to capture short-lived and subtle changes in cortical excitability (De Graaf et al., 2018). A combined TMS-EEG study over the superior occipital lobe has found a ceiling effect of cortical response for above threshold stimulation (Raffin et al., 2020). The authors have, however, not correlated their results to any behavioral changes.

The non-motor area that has been investigated the most in a dose-response fashion with multimodal approaches is the DLPFC. In one TMS-EEG study it could be shown that similar to the occipital lobe, the DLPFC has a lower response than M1 to TMS and that on a group level there was a plateau in excitability as a function of stimulation intensity (Raffin et al., 2020). However, an earlier TMS-EEG study showed a linear increase as a factor of stimulation intensity (Kähkönen et al., 2005). Regarding interleaved TMS and fMRI over DLPFC, results are also highly inconclusive. One study could not find any dose response relationship (Dowdle et al., 2018), while another study revealed that former inconclusive results might be driven by large between-subject variability (Tik et al., 2023b). Also, investigating a group of individuals with schizophrenia, there was no clear dose-response pattern between stimulation intensity and BOLD response close to the stimulated area (Webler et al., 2020). Furthermore, it is suggested that remote areas, rather than solely the stimulated DLPFC show compensatory or reactivity patterns to stimulation intensity (Li et al., 2004; Tik et al., 2023a). In this regard a recent study could show linear increases in subcortical regions as response to different DLPFC responses to increasing stimulation intensities (Tik et al., 2023a).

In terms of dose adjustments for TMS treatment protocols, it has been suggested that the stimulation intensity defined from M1 might be adjusted for scalp-to-cortex distance for regions beyond M1 (Stokes et al., 2013), while newer approaches suggest adjustments of the induced E-field strength (Caulfield et al., 2021; Turi et al., 2022). Based on the studies reviewed here, the distance adjustment approach might be valid for V1 areas and intraparietal sulcus, while other areas, such as the DLPFC, might show a different reaction pattern to stimulation intensities. For DLPFC, combined EEG or fMRI approaches might be employed to identify excitability levels. Concerning BOLD response, however, it remains largely unclear how excitability levels due to stimulation relate to hemodynamic response (Cai et al., 2022). Overall, further research is needed to identify exact excitability patterns to TMS stimulation evaluating behavioral and physiological outputs.

Finally, complex measures of excitation patterns investigating areas beyond M1, including paired-pulse protocols and dual coil TMS, SP, LICI and SICI are rarely or not applied at all considering the different features of non-motor areas and difficulties in applications (Badawy et al., 2014; Derosiere et al., 2020; Hupfeld et al., 2020; Neige et al., 2021; Cash et al., 2017).

Clinical applications

Measuring excitability beyond M1 is of crucial importance for a variety of applications in clinical populations. In terms of migraine and epilepsy, it can help to understand the pharmacological effect of interventions in a more fine-grained manner (e.g. Meisel et al., 2015; Puledda et al., 2023). Furthermore, more circumscribed mapping procedures of (deviant) excitability can help to identify the source thereof especially in focal epilepsy (Moosavi et al., 2022 ; Ramantani et al., 2023). For patients with brain lesions, e.g. after stroke, measures of excitability can help to predict recovery and inform rehabilitation strategies (Joy and Carmichael, 2021; Momi et al., 2025).

Declaration of Competing Interest

EK is a consultant at Nexstim Inc.

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