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# Mobile neuroimaging: What we have learned about the neural control of human walking, with an emphasis on EEG-based research

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ABSTRACT

Our understanding of the neural control of human walking has changed significantly over the last twenty years and mobile brain imaging methods have contributed substantially to current knowledge. High-density electroencephalography (EEG) has the advantages of being lightweight and mobile while providing temporal resolution of brain changes within a gait cycle. Advances in EEG hardware and processing methods have led to a proliferation of research on the neural control of locomotion in neurologically intact adults. We provide a narrative review of the advantages and disadvantages of different mobile brain imaging methods, then summarize findings from mobile EEG studies quantifying electrocortical activity during human walking. Contrary to historical views on the neural control of locomotion, recent studies highlight the widespread involvement of many areas, such as the anterior cingulate, posterior parietal, prefrontal, premotor, sensorimotor, supplementary motor, and occipital cortices, that show active fluctuations in electrical power during walking. The electrocortical activity changes with speed, stability, perturbations, and gait adaptation. We end with a discussion on the next steps in mobile EEG research.

## Introduction

Historically, our scientific understanding of human locomotion has swayed from contrasting perspectives on the importance of the brain for controlling walking and running. For over a century, scientists have debated whether peripheral reflexes, spinal neural networks (e.g., central pattern generators), or brain and brainstem were the most important in determining the basic patterns for human locomotion. As technologies and scientific approaches for studying locomotion have progressed, experimental data and theoretical constructs have increased our appreciation that supraspinal commands, spinal oscillators, and peripheral spinal reflexes all play critical roles in human locomotion (Fig. 1).

The focus on determining the dominant aspect of tripartite neural control of locomotion became very active in the 20th century. The predominant theory in the 17th century was that the striatum was the dominant means of controlling vertebrate locomotion (Molnár, 2004). By the 18th and 19th centuries, scientists better recognized that there was involvement of reflexes and spinal neurons in the control of animal locomotion (Clarac, 2008). However, it was Sherrington's pioneering research at the beginning of the 20th century that showed that walking motions occurred predominantly due to a series of reflex chains (Sherrington, 1910). He demonstrated that decerebrate cats were able to perform gait-like stepping movements despite the lack of input from the brain and offered evidence that peripheral sensory afferents provided the stimulus for stepping behaviors (Sherrington, 1910). Soon after Sherrington's publication, however, Thomas Graham Brown made an argument that rhythmic activation in spinal networks of neurons, rather than reflex responses to sensory inputs, provided the main impetus for locomotor control. Brown deafferented the hind limbs of decerebrate cats and still observed spontaneous rhythmic bursts of activity in flexor and extensor muscles (T. Brown, 1911). He proposed that the activity of mutually inhibitory spinal neurons, made up from flexor and extensor half-centers, produced the stepping rhythm in limbs. Coming at a time when Sherrington's reflex viewpoint held sway in the scientific community, Brown's revolutionary hypothesis found little traction. It was not until the efforts of Lundberg, starting around 1957, that Brown's ideas began to swing the pendulum towards the importance of spinal neural networks in locomotor control (cf. Stuart and Hultborn, 2008). A host of research in the 1960s, 1970s, and 1980s extended Brown's ideas,

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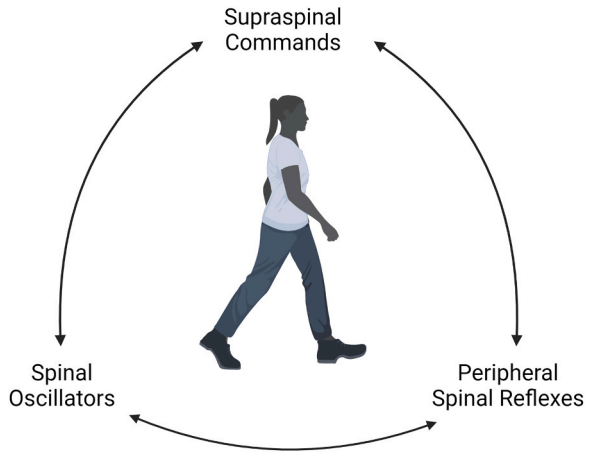


**Fig. 1.** The theories of motor control of human locomotion have swung, much like a pendulum, between supraspinal centers, spinal neural networks, and peripheral reflexes as the predominant contributor to the control of gait across centuries of research. (Figure created using biorender.com)

placing much of the research focus in locomotor control onto spinal neural networks (reviewed in Clarac, 2008). Data from invertebrates demonstrated rhythmic locomotor-like activity from isolated neural networks in animal preparations (Hughes and Wiersma, 1960; Wilson, 1961). Additional studies on cats yielded more evidence that the spinal cord in vertebrates could provide a great deal of the control for stepping in legged locomotion and could even learn to improve its stepping control (Barbeau and Rossignol, 1987; Forssberg and Grillner, 1973; Grillner and Wallén, 1985; Grillner and Zangger, 1979; Lovely et al., 1986). The spinal neural networks capable of generating a rhythmic muscle activation pattern have been termed central pattern generators and have been reviewed extensively by many other authors (Duysens and Van de Crommert, 1998; Grillner et al., 2008; Guertin, 2013).

There were contrasting perspectives, however, on the importance of the brain to neural control of vertebrate locomotion. Shik and Orlovsky's research on cat locomotion was published in English in the 1960s and 1970s (Shik et al., 1966, 1968; Shik and Orlovsky, 1976). They were able to demonstrate that electrical stimulation of neurons in the midbrain could control locomotion onset and speed directly. This led credence to the idea that supraspinal centers dictated the terms of locomotion, leaving spinal pattern generators and reflexes to shape specific muscle activation patterns. In the last two decades, new electrophysiology techniques have revealed even more involvement of the brain in the details of walking control (Drew et al., 2004; Knikou, 2012; Zehr and Stein, 1999). For example, intracortical electrodes reveal that the motor cortex of decerebrate cats elicits step-related frequency modulation during walking (Armstrong and Drew, 1984a, 1984b; Widajewicz et al., 1994). When more complex tasks are performed, such as stepping over an obstacle or traversing uneven terrain, cortical activation increases compared to walking on smooth, even surfaces (Drew et al., 2002; Widajewicz et al., 1994). These findings in cats have focused more attention on the role of the cortex in vertebrate locomotion.

One common proposal has been that humans and other primates exhibit "cortical dominance" of walking compared to other mammalian vertebrates that may be more dependent on spinal oscillators and peripheral reflexes. This is, perhaps, particularly important in relation to the control needs associated with bipedalism and the use of the hands and arms during walking (Fulton and Keller, 1932). Attempts to identify locomotion central pattern generator circuits in non-human primates have been less successful than experiments on other vertebrates (Eidelberg et al., 1981; Fedirchuk et al., 1998; Vilensky and O'Connor, 1997). As such, the relative importance of cortical and other supraspinal vs. spinal mechanisms in human locomotor control may differ markedly from those needed in the control of quadrupedal locomotion.

Studies on humans with neurological deficits have reinforced the importance of supraspinal centers and cortical mechanisms in controlling walking. For example, although patients with injuries to the spinal cord show some evidence of central pattern generators (Bussel et al., 1996; Calancie et al., 1994; Dimitrijevic et al., 1998; Ferris et al., 2004; Kawashima et al., 2008), locomotor training after spinal injury is much less effective in humans than in non-primate animals (van Hedel and Dietz, 2010). Humans with lesions to the premotor or sensorimotor cortex show abnormal gait patterns, particularly when motor adjustments are necessary (Della Sala et al., 2002; Nutt et al., 1993). Studies examining older individuals and neurological patients have found that cognitive deficiencies affect gait dynamics, with executive function and attention being critical aspects of locomotor control (Hausdorff et al., 2007; Laessoe et al., 2008; Sheridan and Hausdorff, 2007; Woollacott and Shumway-Cook, 2002; Yogev et al., 2005; Yogev-Seligmann et al., 2008). All these studies support the idea that everyday real-world locomotion likely depends critically on cortical involvement for successful gait.

A major limitation in the study of human cortical control of locomotion has been the inability to directly measure cortical activity during whole body movement. Unlike animal studies, it is usually unethical to conduct invasive measurements of cortical neurons in human experiment participants. There are human brain imaging modalities that can study cortical activity, but they have historically only been feasible when the human subject is stationary. With recent advancements in hardware and analysis techniques, it is now possible to study brain activity related to whole body movements such as locomotion (Gramann et al., 2011).

This narrative review intends to provide an update on the current understanding of brain involvement in the control of human locomotion for young and neurologically intact individuals. We briefly summarize advantages and limitations of various brain imaging techniques in studying the neural control of human locomotion. We then provide an overview of the recent application of electroencephalography to study electrocortical activity during human locomotion in neurologically intact, young adults. The focus is on what new knowledge has been gained in the last 15 years. The last section provides a prediction of how the next decade will advance our understanding of the neural control of locomotion.

## Brain imaging approaches for studying human locomotion

Many technologies can provide insight into brain activity related to the control of human locomotion. These techniques are summarized in Table 1. The predominant technology for human brain imaging research has been **functional Magnetic Resonance Imaging (fMRI)**. It is an imaging modality that measures brain activity by detecting relative changes in blood oxygenation. fMRI is an indirect measure of brain activity that best correlates with local field potentials (Logothetis et al., 2001). The technique has a spatial resolution within a few millimeters throughout the entire brain but can only detect changes within a few seconds due to its dependence on blood flow (B. He and Liu, 2008). The biggest drawback to using fMRI for studying locomotion is that participants lie supine with their head immobilized during data collection.

Researchers have used fMRI to study brain function related to locomotion by stabilizing the head during rhythmic motions of the legs. Mehta *et al.* designed a pedaling device that was compatible with fMRI to study brain activation during pedaling (Mehta et al., 2009, 2012). Pedaling activates some of the same neural substrates as walking due to its rhythmic motion pattern (Zehr et al., 2007). Participants had bilateral activation of the primary sensorimotor cortices, supplementary motor area, premotor cortex, and cerebellar vermis during pedaling relative to rest periods. Brain activation increased in all the areas with faster pedaling rates (Mehta et al., 2012). The only brain area that showed decreased activation for passive vs. active pedaling was the cerebellum. The authors suggested that much of the observed brain

**Table 1**
Summary of the brain imaging techniques that are used to study human locomotion.

| Brain Imaging Technique | What it measures | Temporal Resolution | Spatial Resolution | Advantages | Disadvantages |
|---|---|---|---|---|---|
| Functional Magnetic Resonance Imaging (fMRI) | Relative changes in blood oxygenation | Second range (limited by hemodynamic response) | Millimeter range | Excellent spatial resolution | Participants must lie supine with the head immobilized |
| Positron Emission Tomography (PET) and Single Photon Emission Computed Tomography (SPECT) | Blood flow using injected radioactive blood tracer | Second range (limited by hemodynamic response) | Millimeter range | Can perform real locomotion with excellent spatial resolution | Low temporal resolution only allows insight into brain activity patterns over long durations |
| Functional Near Infrared Spectroscopy (fNIRS) | Relative changes in blood oxygenation | Second range (limited by hemodynamic response) | Centimeter range, restricted to areas near the scalp | Allows real locomotion | Limited spatial and temporal resolutions |
| Magnetoencephalography (MEG) | Magnetic fields produced by the brain | Millisecond range | Millimeter range | Excellent temporal and spatial resolution | Must be seated and limit movement (may be overcome by optically pumped magnetometers) |
| Electroencephalography (EEG) | Electrical potentials | Millisecond range | Centimeter range, improved with MRI co-registration | Allows real locomotion, excellent temporal resolution | Poor signal-to-noise ratio (overcome with hardware and processing advances)<br>Limited spatial resolution (overcome with MRI co-registration) |

activity during pedaling may be driven by sensory signals from the moving limbs. Other research groups have also developed MRI-compatible devices to study brain activation with rhythmic lower limb movements by supine, stationary participants (Hollnagel et al., 2011; Jaeger et al., 2014; Toyomura et al., 2018). Findings from these studies provide qualitatively similar results with the cycling study of Mehta et al. (2012), and all are limited by the lack of vertical body posture, head and torso movement, balance requirements, and movement variability.

Motor imagery is a more common approach to study control of human locomotion using fMRI. In this paradigm, participants lay down in the scanner and imagine they are walking or running (Hamacher et al., 2015; Jahn, Deutschländer, Stephan, Kalla, Hüfner, et al., 2008; Jahn, Deutschländer, Stephan, Kalla, Wiesmann, et al., 2008; Jahn et al., 2004; la Fougère et al., 2010; Sacco et al., 2006; Stolbkov et al., 2019). Results from these studies have demonstrated that a large number of brain areas show increased activity during imagined locomotion, and that many of the areas show increasing activation with greater locomotor speed. Specifically, there is prominent activation in fusiform and parahippocampal gyri along with activation in the inferior frontal gyri, supplementary motor area, medial and inferior temporal gyri, occipital lobe, and cerebellum. During imagined running, the greatest increase in brain activity with respect to rest occurred in the cerebellar vermis and hemispheres.

Other studies have measured brain activity of real locomotion using molecular imaging techniques, such as **positron emission tomography (PET)** and **single photon emission computed tomography (SPECT)** (Christensen et al., 2000; Fukuyama et al., 1997; Hanakawa, Fukuyama, et al., 1999; Hanakawa, Katsumi, et al., 1999; la Fougère et al., 2010; Malouin et al., 2003; Tashiro et al., 2001). These techniques require intravenous injection of a radioactive blood tracer that is administered prior to performing a task. Blood flow then increases to areas of the brain involved in performing the task, allowing subsequent imaging to identify areas with increased brain activity across the multiple minutes of performing the task. They offer high spatial resolution but low temporal resolution, providing insight into brain activity patterns that happen over long durations while participants perform real locomotion. Results from such studies found consistent activity in primary and supplementary motor areas, basal ganglia, visual cortex, brainstem, and cerebellum. In a direct comparison of imagined locomotion obtained with fMRI and real locomotion obtained with PET, La Fougère et al. (2010) found that while there were many areas of overlapping brain activity between the two tasks, imagined locomotion appeared to be more dependent on supplementary motor cortex and basal ganglia and real locomotion appeared to be more dependent on the primary motor cortex.

Given the results discussed above from fMRI studies of cyclic pedaling and imagined locomotion, it is interesting to contrast PET/SPECT results from real locomotion with PET/SPECT results from pedaling and imagined pedaling. Christensen et al. (2000) showed that active pedaling revealed increased activation in primary and supplementary motor areas, and parts of the cerebellum. However, passive pedaling did not elicit those responses and was found to have cortical activity similar to a resting state. Resembling the findings comparing PET real locomotion data with imagined fMRI data, Christensen et al. (2000) found that imagined pedaling had greater activation of the supplementary motor areas compared to rest.

A portable method for studying changes in brain activity during real locomotion is **functional near infrared spectroscopy (fNIRS)**. Sometimes called optical tomography/imaging, fNIRS is an indirect, optical neuroimaging tool that measures the hemodynamic changes that occur when areas of the brain use oxygen for metabolism. The technique involves shining light into the scalp and measuring the spectra of the light that is reflected. Differences in light spectra correlate with changes in oxygenated and deoxygenated hemoglobin at specific areas across the cortical surfaces (Leff et al., 2011). The mechanism for fNIRS is similar to fMRI as both detect changes in the blood-oxygenation level dependent (BOLD) signal. However, it has a lower spatial resolution than fMRI and is limited to imaging brain areas that are near the scalp. Because the motor regions of the human cortex are near the scalp, fNIRS is suitable for studying the cortical response during complex motor activities. Another advantage is that fNIRS is portable and relatively robust to motion artifacts, which allows the brain to be imaged during whole body movement.

The number of studies on human locomotion using fNIRS technology have been steadily increasing since the start of the 21st century (Bishnoi et al., 2021; Hamacher et al., 2015; Pelicioni et al., 2019; Vitorio et al., 2017). Because of the limited spatial resolution and depth range of fNIRS, comparison between results from fNIRS studies on human locomotion with fMRI or PET/SPECT study results examining brain areas involved in the neural control of human locomotion should be done with reservations. However, fNIRS studies have supported the involvement of prefrontal cortex, premotor and primary motor cortex, supplementary motor cortex, and somatosensory cortex in human walking (Harada et al., 2009; Holtzer et al., 2011; Koenraadt et al., 2014; Kurz et al., 2012; Meester et al., 2014; Metzger et al., 2017; Miyai et al., 2001;

Suzuki et al., 2004, 2008). These studies suggest that prefrontal, supplementary motor, primary motor, and premotor cortices have significantly greater activation at faster walking speeds, but there is some discrepancy in the studies. The contradictory results may be reflective of differences in quantifying oxygenated hemoglobin, deoxygenated hemoglobin, or total hemoglobin metrics as well as varied data processing approaches (Herold et al., 2017; Menant et al., 2020; Vitorio et al., 2017). As described in Menant et al. (2020), measuring changes in oxygenated hemoglobin concentrations represents the direct metabolism of the neural tissues and offers a higher signal-to-noise ratio than deoxygenated hemoglobin, but it is more susceptible to systemic contributions unrelated to the task. It is useful to also provide a measure of change in deoxygenated hemoglobin concentration, which correlates closely with the BOLD signal, and total hemoglobin, particularly since populations such as older adults and neurological patients have pathologies that can affect hemodynamics. Other fNIRS studies suggest increased levels of difficulty or complexity of walking are associated with increased recruitment of prefrontal cortex (Holtzer et al., 2011; Koenraadt et al., 2014; Kurz et al., 2012), but there is also discrepancy in these findings that may be related to the neurological status of the participants (e.g., age, disorders) or conditions of the task (e.g., walking speed, treadmill vs. overground). For a more comprehensive overview of fNIRS-based investigations into the cortical involvement in locomotion please refer to Herold et al. (2017) and Leff et al. (2011).

In addition to its limited spatial resolution and depth range, fNIRS has other disadvantages that limit its usefulness to study human locomotion. As it relies on blood flow and changes in oxygenation levels, systemic changes in cardiac output affect its metrics (Haeussinger et al., 2014; Kirilina et al., 2012). During activities where heart rate and blood pressure are changing across time, brain activity can be difficult to interpret. Fortunately, the addition of reference channels, short-separation channels, and sophisticated data analyses techniques mitigates these limitations (Herold et al., 2017; Leff et al., 2011; Menant et al., 2020). fNIRS also has a low temporal resolution, with changes in blood flow to regions of the brain occurring over several seconds or more (Leff et al., 2011). The hemodynamic response does not occur on a time scale that can capture the within-stride neural dynamics of gait. Lastly, fNIRS does not allow exploration of common electrical connections between the cortex and the muscles (e.g., corticomuscular coherence) which could limit the interpretability of the role of cortical involvement in locomotion.

One brain imaging modality that has high temporal resolution is **magnetoencephalography (MEG).** MEG measures magnetic fields produced by the brain (Hari and Puce, 2017; Vrba and Robinson, 2001). A person sits with their head inside the helmet-shaped device which contains sensors that measure changes in magnetic fields. Participants must stay as motionless as possible to avoid motion artifacts (Hari and Puce, 2017) and like fMRI, the mass and size of the imaging technology prevents normal human locomotion. However, a major advantage of MEG over fMRI for brain imaging is a much greater temporal resolution (milliseconds vs. seconds). So far, it has only been possible to measure imagined locomotion using MEG, however, the recent development of wearable MEG sensors, optically pumped magnetometers, may permit mobile MEG brain imaging during human locomotion (Tierney et al., 2019). Seymour et al. (2021) demonstrated that this tool can be used in mobile settings, although it has not yet been applied to human locomotion. This possibility holds considerable promise for better spatial and temporal resolution of brain activity during human walking and should be seriously considered by investigators considering mobile brain imaging technology for clinical and research purposes.

Another approach to mobile brain imaging with relatively high temporal resolution is **electroencephalography (EEG).** EEG is the recording of electrical potentials generated by the brain using electrodes placed on the scalp (Fig. 2). EEG is a promising tool for mobile brain imaging because it is non-invasive, lightweight, and portable. It directly measures cortical activity compared to other indirect measures, such as the measure of blood flow that reflects neuronal metabolic processes (fNIRS and fMRI). It also provides a very high temporal resolution of brain activity, suitable to measure intra-stride brain involvement in real locomotion. However, a major limitation of utilizing EEG during whole body movement is the very poor signal-to-noise ratio. The amplitude of the recorded electrocortical signals is very small and they are often obscured by large motion and muscle artifacts generated during whole body movement, such as walking (Castermans et al., 2014; Gwin et al., 2010; Kline et al., 2015; Oliveira et al., 2016; Snyder et al., 2015; Symeonidou et al., 2018). With advancements in hardware and signal processing approaches to mitigate artifacts, EEG has become an increasingly popular modality to study cortical brain involvement in real human locomotion. While fNIRs, fMRI, SPECT, PET, and MEG provided some insight into brain involvement in human locomotion, EEG is the only modality thus far that has allowed intra-stride resolution insight into electrocortical dynamics of real human locomotion. The following sections take a deeper dive into EEG as a brain imaging tool to investigate human walking in young, neurologically intact populations. We provide an overview of the initial attempts to investigate human locomotion, highlighting the limitations of early works. We then discuss recent advances which have allowed for improved fidelity and rigor of EEG to study human locomotion. The focus is on highlighting the common consensus findings that improve our understanding of human brain involvement in locomotor control in neurologically intact individuals. Finally, we propose some potential next steps in mobile brain imaging research with EEG.

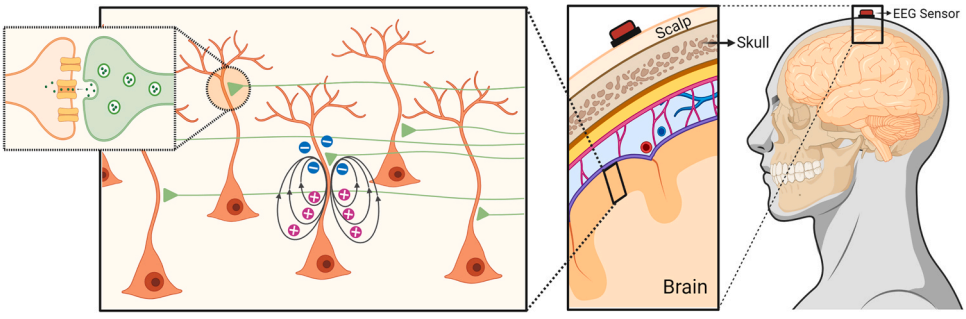


**Fig. 2.** Scalp electroencephalography (EEG) is a non-invasive method used to record electrical activity in the brain. This activity is captured via electrodes placed on the scalp, which detect tiny (10–100 μV) electrical charges resulting from the activity of pools of neurons. Neurons communicate with each other through electrical impulses and chemical signals, creating electrical activity that EEG can measure. While the potential of a single neuron is undetectable with scalp EEG, a large population of neurons with synchronized activity can produce far field potentials that propagate to the scalp. (Figure created by Seongmi Song using biorender.com).

## The neuroimaging of human locomotion with electroencephalography

### *Electroencephalography explained*

Scalp EEG measures electrical activity from cortical structures beneath the skull (Fig. 2). Neurons communicate through synapses and oscillations in electrical currents, propagating information about commands, sensation, and computation. When a neuronal action potential fires, it creates a postsynaptic potential across the synapse (Teplan, 2002). Although the potential of a single neuron is undetectable with EEG, the summation of a large population of neurons is strong enough to produce far field potentials that propagate to the scalp from parallel aligned neurons. The EEG signal comes primarily from post-synaptic currents (~80% of EEG signal) and action potentials (~20% of the EEG signal) (Thio and Grill, 2023). Activity of pyramidal neurons in the cortex dominate the signals recorded at the scalp for EEG (Hari and Puce, 2017; Teplan, 2002). These cells are oriented perpendicular to the cortical surface and generate electrical currents which are either toward or away from the scalp (Hari and Puce, 2017). The summation of activity due to this stable orientation allows this activity to be detectable through EEG, while nonpyramidal cells in deeper structures contribute less to the measurable signals (Hari and Puce, 2017). Although these deeper neurons might also be working synchronously, it is challenging to observe this through EEG recordings. The folds of the cortex alter the orientation of the neurons relative to the scalp and influence whether the potentials reach the scalp (Scherg et al., 2019). Recent research suggests that under ideal, stationary conditions it may be possible to record EEG sources from basal ganglia and cerebellum (Andersen et al., 2020; Samuelsson et al., 2020; Seeber et al., 2019; Tzvi et al., 2022), but there is little evidence yet that this resolution is realistic for mobile EEG.

Changes in EEG signals are often quantified in terms of synchronization and desynchronization (Pfurtscheller and Lopes da Silva, 1999). **Synchronization** refers to instances when a neuronal population produces more congruent timing of postsynaptic potentials relative to a baseline state, or when there is an increase in the number of neurons that are contributing to the congruent timing of postsynaptic potentials relative to a baseline state. **Desynchronization** refers to instances when a neuronal population produces less congruent timing of postsynaptic potentials relative to a baseline state, or when there is a decrease in the number of neurons that are contributing to the congruent timing of postsynaptic potentials relative to a baseline state. There are two critical aspects of those definitions. First, there is not a direct correlation from the synchronization/desynchronization axis to more/less brain activity as it is often presumed in fMRI and fNIRS studies (Hermes et al., 2017; Hipp and Siegel, 2015; Winterer et al., 2007). Desynchronization in EEG can come from contributing neurons that are more independent in the firing timing, or it can come from having fewer contributing neurons at the same level of congruent firing timing. Attempts at identifying a universal transfer function between EEG spectral power and BOLD signal power have not been successful.

The frequency of EEG signal power has long been an indicator of different brain states when humans are at rest (Teplan, 2002). The five typical frequency bands of EEG are: **delta** (<3.5 Hz), **theta** (4–7.5 Hz), **alpha** (8–13 Hz), **beta** (14–30 [or 40] Hz), and **gamma** (>30 [or 40] Hz) (Hari and Puce, 2017). Scalp EEG electrodes located over the sensorimotor cortex have identified a strong central alpha signal (and sometimes lower frequency beta signal) that is designated the "**mu** rhythm" (Gastaut, 1952). Different frequency bands are thought to be correlated with certain behavioral mental states in human participants. For example, wakeful relaxation evokes alpha activity emanating from the occipital cortex, which becomes very prominent with eyes closed (Adrian and Matthews, 1934; Berger, 1929; Jasper, 1936; Smith, 1938). Planning and executing an upper limb motor task results in desynchronization in the mu rhythm over the sensorimotor cortex, presumably because the neurons involved are actively computing neural commands for the movement. Hence, it has often been assumed that desynchronization in a cortical area of interest is related to increased computation and involvement relative to the comparison state (Pfurtscheller, 1992). There is evidence that all the frequency bands are likely to convey meaningful information about the control of walking (Gwin et al., 2011; Nakagome et al., 2020; Presacco et al., 2011; Seeber et al., 2014, 2015; Sipp et al., 2013; Wagner et al., 2016).

Brain activity can also be analyzed as **event-related potentials** that are time-locked to a stimulus (Luck, 2014). An evoked potential is a fluctuation in voltage that was caused by an external or internal stimulus (Bickford, 1987; Nunez and Srinivasan, 2006; Teplan, 2002). Event-related potentials are extracted by averaging epochs of EEG that are time-locked to an event (Gevins and Rémond, 1987; Teplan, 2002). Any spontaneous fluctuations unrelated to the event are averaged out, leaving only the activity which is consistently associated with the processing of the stimulus (Teplan, 2002). **Event-related spectral perturbations** are, similarly, an averaging of epochs of EEG data that are time-locked to an event but have been Fourier transformed to reveal the power spectral density of the signal (Makeig, 1993). EEG walking data are often displayed in event-related spectral perturbation graphs which typically cover a gait cycle, from one heel strike to the next, and present the changes in spectral power at frequencies of interest (Fig. 3). Spectral power is often illustrated by a gradient of colors. In Fig. 3, green represents no change, red represents an increase in power, or synchronization, and blue represents a decrease in power, or desynchronization.

In the processing of EEG data, it is important to select an appropriate baseline to isolate the oscillations of interest (Makeig et al., 2004; Onton et al., 2006). For example, when comparing walking to standing we can see a general reduction in spectral power (Severens et al., 2012). Irrespective of this overall change, there are modulations in postsynaptic potential that will occur throughout a gait cycle. To properly interpret synchronization and desynchronization that occur during a gait cycle, we must therefore isolate these changes by selecting an appropriate baseline. Choosing a baseline state for comparison influences conclusions about whether there is an increase or decrease in synchronization or desynchronization. Different scientific questions require different baseline comparisons. For example, examining how electrocortical activity changes across walking speeds in a specific set of individuals would require a different baseline comparison than examining whether there is more synchronization or desynchronization in a given brain area during walking for a neurologically intact group of participants compared to a group of participants with neurological deficits. This is

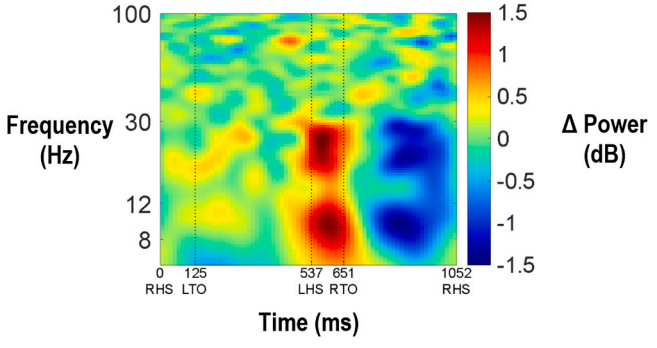


**Fig. 3.** Example of an event-related spectral perturbation graph, representing the changes in spectral power in different frequency bands over time. While examining walking, gait events are often represented on the x-axis. In this case, the graph covers one gait cycle starting at right heel strike (RHS) followed by left toe off (LTO), left heel strike (LHS), right toe off (RTO), and ends with the second RHS. Green represents no change in spectral power, red represents an increase in power (i.e. greater synchronization), and blue represents a decrease in power (i.e. greater desynchronization). Note that this graph does not represent biological data but simulated activity from a neural mass model (Richer et al., 2020).

because the baseline state of the neurologically intact group could be different than the group with neurological deficits, thus we need to isolate brain activity that is involved in walking from the differing baseline states caused by health status. Most of the time, EEG changes in synchronization/desynchronization within a given experiment are good local indications of brain involvement but may not reflect a universal standard of brain involvement for the task and condition.

*Advances in EEG hardware and processing*

In recent years, there has been substantial development of EEG hardware and data processing algorithms (Gramann et al., 2011; Makeig et al., 2009). Miniaturization of amplifiers, active electrodes, and active shielding techniques have all reduced noise corruption on mobile systems (Niso et al., 2023). Mobile and high-density systems, involving 128 or more electrodes, now offer the opportunity to collect high-quality data during movement. It is helpful to have reference signals such as electrooculography, eye-gaze tracking, electrocardiogram, electromyogram, and motion sensors (Hari and Puce, 2017). For instance, one recent improvement is the development and validation of a dual-electrode EEG system which allows the user to better isolate electrocortical activity from motion artifact (Nordin et al., 2018). The adapted system contains an inverted secondary layer of electrodes which are mechanically coupled but electrically isolated from the scalp sensors. They are covered by a conductive fabric to create an artificial skin. While the scalp electrodes record electrocortical activity, physiological signals, and motion artifact, the secondary electrodes only record motion artifact. The common motion artifact in both scalp and noise channels allows a more efficient cleaning of scalp channels. Similarly, experimenters can rely on electromyography electrodes placed on the neck to record reference muscle activity signals and help isolate the muscle artifact from electrocortical signals (Bradford et al., 2016; Nordin et al., 2019, 2020).

Data processing algorithms for electrophysiological source separation has greatly improved in recent years (B. He et al., 2018). One method frequently used to isolate artifacts from electrocortical activity is **blind source separation** (Fig. 4). The potentials that are recorded at the scalp originate from various sources in the brain and often overlap. Each electrode will therefore record a mixture of several different sources. Blind source separation separates these mixed signals into components (sources), like the way we can detect an individual voice in a crowd full of talking people. **Independent component analysis**

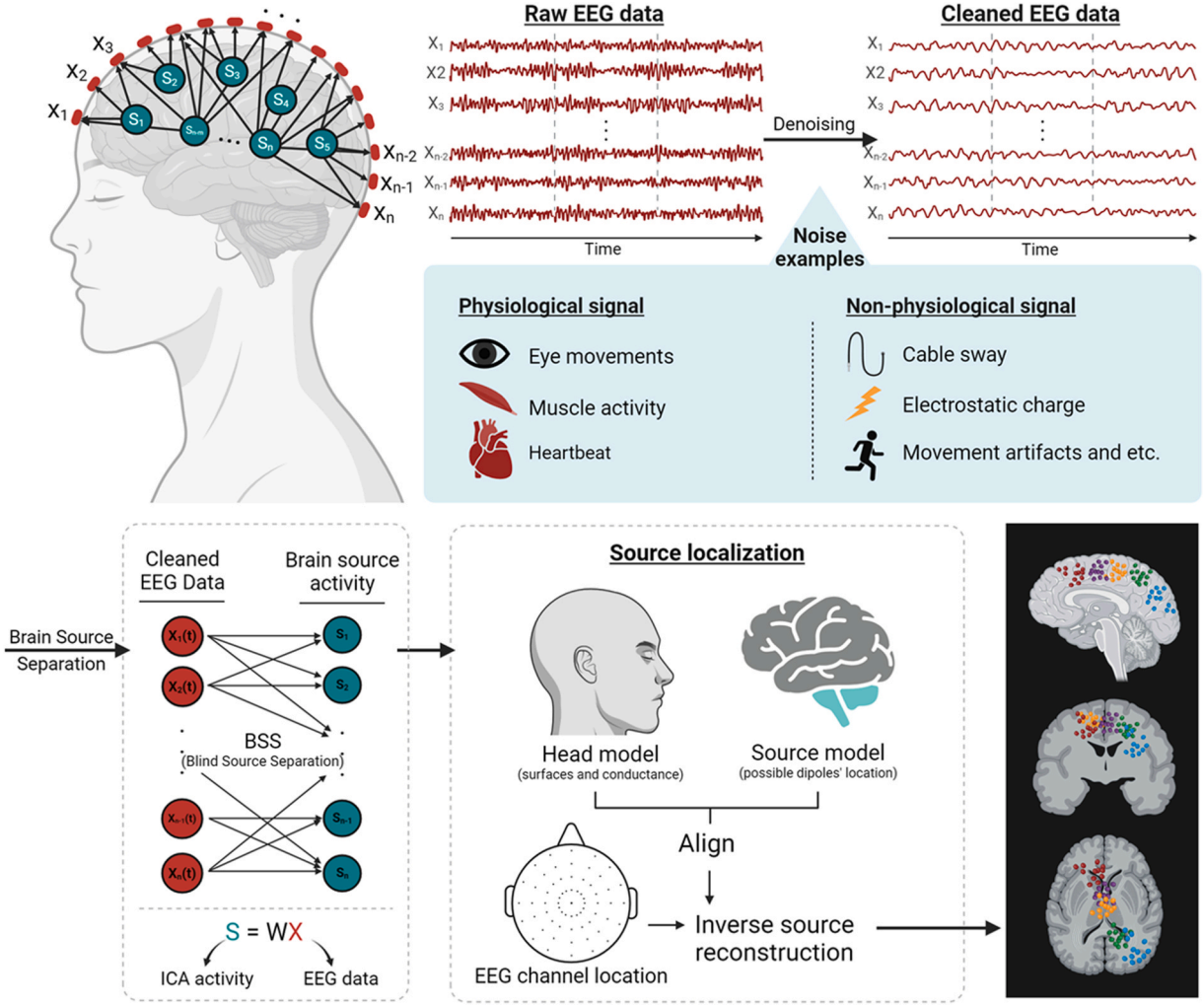


**Fig. 4.** This figure presents a high-level example of EEG preprocessing steps. Scalp EEG measures a mixture of many electrical potentials generated within or near the body in addition to the brain signals of interest. Recording EEG during whole body motion, such as locomotion, can increase or add non-brain signal sources such as cable sway and movement-related sensor noise. As an initial step, many EEG researchers start by filtering and denoising their data. There is a large body of literature on different approaches for denoising raw EEG data, and while there is no consensus on the best approach, careful consideration should be taken when cleaning and interpreting EEG in mobile scenarios. To further improve the interpretability of the recorded signals, brain source activity can be disentangled from the scalp EEG using approaches like independent component analysis (ICA). If using high-density scalp EEG, inverse source reconstruction can be performed to approximate the three-dimensional locations of active brain sources within the brain volume with about 1 cm accuracy. (Figure created by Seongmi Song using biorender.com).

(**ICA**), the most common method (Hari and Puce, 2017), separates the signal into components that are independent from each other (Delorme and Makeig, 2004; Hyvärinen and Oja, 2000; Jung et al., 2000; Makeig et al., 1996). ICA is useful because it can isolate non-brain sources, such as muscles, eyes, and heart, which can later be removed through processing (Fig. 4) (G. D. Brown et al., 2001; Hari and Puce, 2017; Vigário, 1997; Vigário et al., 2000). It can also distinguish between various brain signals, evoked responses, and brain rhythms (Hari and Puce, 2017). Although many blind source separation methods are available, **adaptive mixture independent component analysis (AMICA)** (Palmer et al., 2012) has been shown to be one of the most efficient algorithms (Delorme et al., 2012). Processing algorithms such as **PowPowCAT** can help with classification of these independent components (Thammasan and Miyakoshi, 2020).

Other approaches have been used to remove muscle artifact, such as **canonical correlation analysis** (De Clercq et al., 2006; Gao, Zheng, et al., 2010; Vergult et al., 2007), **empirical mode decomposition** (Mijović et al., 2010), and **wavelet transforms** (Aminghafari et al., 2006; Estrada et al., 2011; Gao, Sultan, et al., 2010; Indiradevi et al., 2008; Iyer and Zouridakis, 2007; Krishnaveni et al., 2006). Safieddine et al. (2012) compared four methods for elimination of muscle artifact (ICA, canonical correlation analysis, empirical mode decomposition, and the wavelet transform). They show that performance of these methods depends on the amplitude of muscle contamination. Head phantom experiments can help validate the use of these methods for specific types of data sets. For example, canonical correlation analysis was shown to help isolate simulated brain signals from neck muscle activity during walking head movements (Richer et al., 2020). A recent extension of canonical correlation analysis for EEG artifact removal is the **iCanClean** algorithm (Gonsisko et al., 2023), which can be used both with dual electrode and single electrode EEG systems.

**Artifact Subspace Reconstruction** is one useful method to remove motion artifacts. Its effectiveness has been demonstrated in multiple experiments (Artoni et al., 2017; Chang et al., 2018; Luu, Brantley, Nakagome, et al., 2017; Luu, Nakagome, et al., 2017; Mullen et al., 2013; Nordin et al., 2020; Peterson and Ferris, 2018). It uses an approach based on Principal Component Analysis to interpolate high variance components that exceed a predetermined threshold relative to a clean EEG dataset (Chang et al., 2018; Mullen et al., 2013). The artifact detection threshold must be carefully selected because aggressive cutoffs can remove brain activity along with artifacts (Artoni et al., 2017; Chang et al., 2018; Richer et al., 2020).

There is not a single data cleaning approach that is ideal for all data conditions and experiments. The relative ratios and magnitudes of muscle, eye, brain, and motion artifact, and the temporal nature of the signal components (e.g., rhythmic, discrete), influence the success of different data pre-processing methods (Safieddine et al., 2012). Under relatively low levels of motion and muscle artifact, it has been argued that minimal to zero pre-processing is actually best for large data sets (Delorme, 2023). Our experience is that large amounts of muscle and motion artifact require aggressive methods to remove artifacts, as demonstrated by electrical head phantom validation studies (Nordin et al., 2018, 2019; Oliveira et al., 2016; Peterson and Ferris, 2019a; Richer et al., 2020). As a result, a combination of approaches is often used to reduce artifacts and isolate brain signals in scalp EEG during walking and running.

When using a greater number of channels, EEG allows us to perform source localization to estimate the location of the active brain sources (Fig. 4). It is important to note the challenges and assumptions involved in source-based analysis. When we estimate the location of cortical sources, we face the forward problem and the inverse problem. The **forward problem** is to find the scalp potentials that are produced by sources in the brain (Hallez et al., 2007; B. He et al., 2018; Michel and He, 2012, 2019). These electrical currents propagate through various tissues (scalp, skull, cerebrospinal fluid, brain), and these tissues have varying levels of conductivity that attenuate the current to different extents. Thus, we model the head geometry to help solve the forward problem. The current ideal method is to use individual MRI to precisely model the shape of the head and the thickness of tissues.

The **inverse problem** refers to the challenge of determining the location of the brain sources that generate an EEG measurement (B. He et al., 2011; Michel and He, 2019; He et al., 2018; Michel and He, 2012; Grech et al., 2008). A solution can be found if a priori assumptions about the sources are included, such as neurophysiological, biophysical, and anatomic knowledge about the sources, electrical activity, conductive tissues, and distribution of the neuronal activity (Michel and He, 2019). There are various methods that can be used to solve the inverse problem. There is not one best way yet to solve it, but multiple studies suggest that state of the art methods result in a spatial resolution of about 1 cm for identifying brain sources from scalp EEG (Acar et al., 2008; Akalin Acar and Makeig, 2013; B. He et al., 2011; Seeber et al., 2019).

It is possible to increase EEG's spatial accuracy by increasing the number of electrodes on the scalp. In source-level analysis, the number of dipoles we can find is limited by the number of electrodes, therefore a higher-density setup will allow a better estimation of locations and strengths of electrocortical activity (B. He et al., 2011). To correctly identify sources, it is also important to know the exact location of electrodes in relation to the person's head. These positions can be applied to simplified head model templates or co-registered to an individualized structural MRI scan to position the sensors in relation to each person's brain anatomy (Hari and Puce, 2017). A recent study compared the different localization methods and suggested that using MRI scans, when possible, will lead to more accurate source localization (Liu et al., 2023).

### *Initial investigations of electrocortical activity during locomotor patterns*

Because of its sensitivity to artifacts, initial attempts to use EEG to probe the involvement of cortical structures in human locomotion used models of locomotion, rather than actual locomotion. Raethjen et al. (2008) found that rhythmic EEG was directly related to rhythmic foot movements during seated postures. Wieser et al. (2010) studied participants on a tilt table performing rhythmic leg motions. They found that EEG amplitude in cortical motor areas was modulated throughout the movement cycle. The authors of both studies propose that these fluctuations in electrocortical activity may be present during locomotion.

Pedaling/cycling has also been used to model locomotion brain dynamics (Jain et al., 2013; Schneider et al., 2013). Like walking, it is a cyclical locomotor activity, but it does not require balance or open-ended interlimb coordination. Pedaling/cycling also generates less motion artifact than walking, which can be beneficial. Modulations in electrocortical signals across the pedaling cycle over sensorimotor (Jain et al., 2013) and motor (Schneider et al., 2013) cortical regions of the legs were correlated to muscle activity of the legs (Schneider et al., 2013). Peak-to-peak amplitude of the EEG waveform was greater in passive compared to active pedaling at a matched speed (Jain et al., 2013). A similarity in electrocortical fluctuations in active and passive pedaling suggests that much of the EEG waveform is dedicated to processing of sensory information (Jain et al., 2013). The decrease in amplitude during active pedaling could be explained by a gating of sensory input by corticospinal motor output (Jain et al., 2013). There are, however, differences in electrocortical oscillations of walking and cycling (Storzer et al., 2016).

Due to general acceptance of event-related potential studies on human cognition using EEG, initial attempts at electrocortical recordings during walking focused on recording event-related potentials like the P300 during human locomotion. The P300 is named after a positive waveform 300 ms following a stimulus. It is an event-related potential that can be elicited with visual or auditory discriminations tasks, such as an oddball task. The use of EEG to recover electrocortical dynamics during actual locomotion was first validated by having participants walk and run while performing tasks that elicited a P300 (De

Sanctis et al., 2012; Debener et al., 2012; Gramann et al., 2010; Kerick et al., 2009). These studies showed that it was possible to extract a normal P300 signal relative to the discrimination task during human locomotion. Advances in EEG hardware and processing have since made it possible to investigate more complex electrocortical dynamics associated with actual locomotion. Please refer to Table 2 for a summary of the experiments discussed in this review.

*Spectral fluctuations of electrocortical activity during walking*

Imaging electrocortical activity in the brain during human walking can provide an indication of which brain areas show synchronization to the gait cycle. The millisecond precision of EEG allows us to observe fluctuations in electrocortical activity throughout the gait cycle rather than averaging over many steps. It wasn't until about the mid-1980s that scientists began speculating in writing that the motor cortex would be involved in the control of locomotion (Armstrong, 1986), but even then, their perspective was "we are almost entirely ignorant as to precisely how the motor cortex (MC) may intervene in the locomotor process." (Armstrong, 1986). As depicted in Fig. 5, the advent of mobile EEG allows us to study human walking and has led to the knowledge that the motor cortex and many other brain areas appear to be involved in monitoring or controlling human walking. It is difficult with observational experimental paradigms to discern the difference between cortical electrical activity involved in receiving sensory feedback about locomotion and cortical electrical activity involved in controlling locomotion.

During normal walking, there is gait-related electrical activity in many different brain areas responsible for sensorimotor processing. Electrocortical power fluctuations occur in the anterior cingulate, posterior parietal, prefrontal, premotor, supplementary motor, occipital, and/or sensorimotor cortices during human walking (Artoni et al., 2017; Bradford et al., 2016; Bulea et al., 2015; Cheron et al., 2012; Gwin et al., 2011; Nordin et al., 2020; Oliveira et al., 2017; Roeder et al., 2018; Seeber et al., 2014; Severens et al., 2012; Yokoyama et al., 2021; Zhao et al., 2022). There is even a recent report of gait-related electrocortical fluctuations in the thalamus and cerebellum (Zhao et al., 2022), but it is difficult to validate and verify that the identified electrical activity is not derived from muscle or other brain areas given the deep location of the thalamus and cerebellum. Many of the areas show a common pattern of increased synchronization during periods of double support and increased desynchronization during limb swing. There are differences across brain regions, but relative to the overall background brain activity, the fluctuation pattern appears.

Another common finding across studies is a lateralization of alpha and beta spectral power fluctuations in motor/sensorimotor cortices related to the gait cycle (Fig. 6) (Bradford et al., 2016; Cheron et al., 2012; Gwin et al., 2011; Jacobsen and Ferris, 2023a; Nordin et al., 2020; Seeber et al., 2014; Severens et al., 2012; Zhao et al., 2022). The motor and sensorimotor cortex sources typically demonstrate increased desynchronization during contralateral limb swing and increased synchronization during ipsilateral heel strike and the subsequent double support period (Bradford et al., 2016; Jacobsen and Ferris, 2023a; Nordin et al., 2020; Severens et al., 2012; Zhao et al., 2022). The pattern of alpha and beta desynchronization and synchronization in the sensorimotor cortex during the gait cycle could be interpreted in many ways. Studies on discrete upper limb movements have long revealed sensorimotor cortex desynchronization prior to movement initiation and synchronization after movement completion in the contralateral hemisphere (Neuper et al., 2006; Pfurtscheller and Lopes da Silva, 1999). This relationship appears to hold true during rhythmic finger movements, albeit with additional long-lasting sensorimotor desynchronization relative to rest (Seeber et al., 2016). However, during walking all four limbs display rhythmic muscle activation patterns with multiple synergies (Davis and Vaughan, 1993; Ivanenko et al., 2004). There are no clear on and off phases during walking due to the large number of muscles involved in locomotion and their periodic phasing of activity. Trying to relate synchronization and desynchronization phasing in the sensorimotor cortex to gait phases based on an assumption of direct muscle control is inappropriate (Delval et al., 2020).

A more appropriate framework for interpreting sensorimotor synchronization and desynchronization phases during human walking might be in evoked beta band spectral power fluctuations based on afferent feedback from gait events (Jensen et al., 2019; Roeder et al., 2018, 2020). Cutaneous and proprioceptive feedback provides strong cues about the stepping pattern both at the spinal cord level and in the brain (Lam and Pearson, 2002; Pearson et al., 1998). The rhythmic oscillation in sensorimotor cortex electrical activity could be due to afferent feedback on gait events as well as ongoing oscillations in spinal circuits related to locomotion. This perspective would be consistent with measures of human electrocorticography in the motor cortex during stepping (McCrimmon et al., 2018; Starkweather et al., 2023). Passive stepping motions induced by a robotic gait orthosis on neurologically intact human participants show sensorimotor cortex beta fluctuations that are similar but less pronounced than active stepping within the orthosis (Wagner et al., 2012). Increases in walking speed attenuate sensorimotor spectral power fluctuations (Bulea et al., 2015; Lisi and Morimoto, 2015; Nordin et al., 2020). This finding is consistent with the idea that the sensorimotor cortex has tonic involvement with locomotion that increases with speed, and afferent feedback about gait cycle timing (especially the rapid gait events around double support beginning and ending) triggering phasic synchronization and desynchronization with the gait cycle. Switching from a normal treadmill to a user-driven treadmill that requires greater horizontal drive produces overall more desynchronization in sensorimotor cortices, suggesting that the user-driven treadmill requires a greater tonic drive from the cortex compared to a motor-driven treadmill (Bulea et al., 2014). Bradford et al. (2016) examined treadmill walking on the level and at a 15% incline. They reported differences in theta spectral power was greater for incline walking in the anterior cingulate, sensorimotor, and posterior parietal clusters. Although the increase was distributed across the entire gait cycle, it was greater at heel strike and toe off. These results suggest that theta power increased in response to the greater motor demands, particularly in periods of transition in the gait cycle (Bradford et al., 2016). These findings are supported by the work of Luu *et al.* (Luu, Brantley, Nakagome, et al., 2017; Luu, Brantley, Zhu, et al., 2017). They compared level-ground, slope, and stair walking and found consistent evidence for changes in theta, alpha, and beta spectral power in keeping with the interpretation described above.

Cortical involvement appears to increase in proportion to the amount of active stability control required for walking. When walking with external lateral stabilization, beta spectral power in the premotor cortex is increased compared to normal walking (Bruijn et al., 2015). This suggests that beta power is related to gait stability and that walking with stabilization requires less motor control (Bruijn et al., 2015). Sipp et al. (2013) investigated cortical contributions to walking stability by asking participants to walk on a treadmill-mounted balance beam. Compared to flat walking, beam walking elicited an increase in spectral power in the theta band in the anterior cingulate, anterior parietal, superior dorsolateral-prefrontal, and medial sensorimotor cortex, and a decrease in spectral power in the beta band for both the left and right sensorimotor cortices (Sipp et al., 2013). Interestingly, before participants fully lost their balance during beam walking, there was an increase in theta band in the anterior and posterior cingulate, superior dorsolateral-prefrontal, anterior parietal, and the left and right sensorimotor cortices. The first increase occurred in the left sensorimotor cortex of right hand and foot dominant individuals during the last double support phase immediately preceding the loss of balance. These changes in electrocortical activity show that there are several regions that are involved in recognizing a loss of balance. This highlights the fact that much of the cortical contributions to gait are involved in sensory processing and will occur when we need sensory information to adjust

**Table 2**
Summary of the EEG experiments discussed in the four following sections: Initial investigations of electrocortical activity during locomotor patterns, spectral fluctuations of electrocortical activity during walking, corticocortical and corticomuscular coherence during walking, and invasive EEG.

| Reference | Task | Manipulation/ Condition | Number of participants (Age) | # EEG sensors (* Denotes invasive sensors) | EEG channel or Source domain analysis | Neural features/ metrics analyzed | Contribution/Major finding |
|---|---|---|---|---|---|---|---|
| **Initial investigations of electrocortical activity during locomotor patterns** | | | | | | | |
| Raethjen et al., (2008) | Seated, rhythmic foot movements | In phase, out of phase, unilateral | 10 (range 25–38 years) | 64 | Channel | Spectral power, corticomuscular coherence | Rhythmic EEG, and thus the cortex, is involved in producing gait like, rhythmic foot movements. |
| Wieser et al., (2010) | Assisted, rhythmic whole leg movements on a tilt table at 76% elevation | Rest, assisted, active, passive | 20 (mean 28.6 ± 8.3 years) | 64 | Channel and source | Movement-related potential, spectral power | EEG in motor cortical areas (primary motor cortex, premotor cortex, supplementary motor area, etc.) are modulated throughout the gait cycle, with the greatest activation at changes of direction of flexion/extension. |
| Jain et al., (2013) | Pedaling on a custom device | Active, passive | 10 (range 22–32 years) | 64 | Channel and source | Pedaling-related potential, spectral power, source localization | EEG in motor cortical areas fluctuates depending on the phase of the pedaling cycle. Pedaling-related potentials have a greater amplitude during passive than active pedaling, suggesting much of the activity is related to sensory perception. |
| Schneider et al., (2013) | Pedaling on a cycle ergometer | Pedaling at different power outputs | 8 (mean f: 24 ± 2 years, m: 27 ± 4 yrs) | 32 | Source | Current density | EEG in motor cortical areas is dependent on exercise intensity and suggests the cortex is involved in controlling muscular effort during locomotor-like activities. |
| Storzer et al., (2016) | Cycling and overground walking | Cycling vs. walking | 14 (mean 24.9 ± 3 years) | 18 | Channel | Spectral power, event-related spectral perturbations | There are differences in EEG of walking and cycling, but both have activity that fluctuates with the gait cycle. |
| De Sanctis et al., (2012) | Sitting and treadmill walking | Go/no-go cognitive task | 5 (mean 24.6 ± 4.8 years) | 72 | Channel | Event-related potentials, spectral power | Robust ERP waveforms can be recorded during slow and fast walking on a treadmill. P300 and ERN were similar across sitting, slow, and fast walking. |
| Debener et al., (2012) | Sitting and overground walking outdoors | Auditory oddball cognitive task | 16 (mean 27.9 years) | 14 | Channel | Event-related potentials | Good quality EEG signals can be obtained during outdoor walking. Smaller P300 amplitude walking outdoors compared to sitting indoors. |
| Gramann et al., (2012) | Treadmill standing, walking, and running | Locomotion speed, visual oddball cognitive task | 12 (mean 24.2 ± 3.4 years) | 248 | Source | Spectral power, event-related potentials, event-related spectral perturbations | Demonstrated reliable measurement and source modeling of brain dynamics during walking at various speeds. |
| Kerick et al., (2009) | Treadmill walking and standing | Walking speed, auditory oddball cognitive task | 5 (range 27–39 years) | 32 | Channel | Event-related potentials, spectral power | Walking and jogging decreased EEG signal quality. N1 and P300 were recoverable while walking but not during jogging. |
| **Spectral fluctuations of electrocortical activity during walking** | | | | | | | |
| Artoni et al., (2017) | Treadmill walking | 3.5 km/h | 11 (mean 30 ± 4 years) | 64 | Source | Event-related spectral perturbations, corticomuscular connectivity (discussed in section on corticocortical and corticomuscular coherence during walking) | Stronger gait locked spectral perturbations in motor related areas than non-motor related areas. ERSPs for the motor-related areas (premotor cortex, motor, supplementary motor, and cingulate areas of the left and right hemispheres) exhibited significant |

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**Table 2** (*continued*)

| Reference | Task | Manipulation/ Condition | Number of participants (Age) | # EEG sensors (* Denotes invasive sensors) | EEG channel or Source domain analysis | Neural features/ metrics analyzed | Contribution/Major finding |
|---|---|---|---|---|---|---|---|
| | | | | | | | desynchronization and synchronization in mu and beta frequency bands respectively during single- and double-foot support phases. |
| Bradford et al., (2016) | Treadmill walking | Walking on incline (15% grade) | 20 (mean 23.1 ± 3.9 years) | 256 | Source | Event-related spectral perturbations, spectral power | Increased theta band spectral power during incline walking in the anterior cingulate, sensorimotor, and posterior parietal regions. Increase theta band power fluctuations at heel strike and toe off during incline walking. Suggests that walking on an incline may involve supraspinal input. |
| Bulea et al., (2014, 2015) | Treadmill walking | User-driven vs. passive treadmill walking, slow and fast speed | 10 (mean 28.9 ± 6.3 years) | 64 | Source | Event-related spectral perturbations, spectral power | Spectral power and spectral fluctuations were attenuated with gait speed. User-driven treadmill produced more desynchronization in sensorimotor cortices. Suggests greater cortical drive during faster speeds and simulated overground walking (user-driven treadmill). |
| Gwin et al., (2011) | Treadmill walking | Speed (standing, 0.8, 1.25, 1.9 m/s) | 8 (range 21–31 years) | 248 | Source | Event-related spectral perturbations, spectral power | Significant intra-stride fluctuations in spectral power in the anterior cingulate, posterior parietal, and sensorimotor cortex. Results suggest cortical involvement in steady-speed human locomotion. |
| Nordin et al., (2020) | Treadmill walking | Speed (0.5, 1, 1.5, 2.0 m/s) | 9 (mean 27.4 ± 4 years) | 128 (dual-layer EEG) | Source | Event-related spectral perturbations, spectral power | Synchronous spectral power fluctuations in the left and right sensorimotor cortices corresponding with the gait cycle. Reduced durations and frequency bandwidth of synchronous power fluctuations at faster gait speeds. Alpha and beta band power increased during contralateral limb single support and push off. Reduced sensorimotor beta and alpha band spectral power at faster gait speeds. Results suggest greater cortical involvement at faster gait speeds compared to slow walking. |
| Oliveira et al., (2017) | Treadmill walking | Walking with eyes open and eyes closed | 10 (range 21–36 years) | 256 | Source | Event-related spectral perturbations | Increase theta band desynchronization in the frontal and premotor cortices during stance and greater desynchronization in theta, alpha, and beta bands during single-support in left and right somatosensory cortex. Data suggest changes in sensory inputs for maintenance of walking when vision is limited. |

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**Table 2** (*continued*)

| Reference | Task | Manipulation/ Condition | Number of participants (Age) | # EEG sensors (* Denotes invasive sensors) | EEG channel or Source domain analysis | Neural features/ metrics analyzed | Contribution/Major finding |
|---|---|---|---|---|---|---|---|
| Seeber et al., (2014) | Active walking and upright standing in a robotic gait orthosis | 1.8–2.2 km/h (adjusted to leg length) | 10 (mean 25.6 ± 3.5 years) | 120 | Source | Event-related spectral perturbations, gait phase modulation | Suppression of upper mu and beta oscillations in active walking vs. standing suggests a movement-related state change of cortical excitability. Beta suppression in central sensorimotor areas, consistent with the location of the lower extremities in the motor cortex. Low gamma amplitudes modulated in relation to the gait phase, represent the motion sequence timing during gait. |
| Severens et al., (2012) | Treadmill walking | Slow speeds @ 1.4 Hz frequency | 6 (mean 21.6 ± 2.3 years) | 62 | Channel | Event-related spectral perturbations, event related desynchrony | Significant mu and beta band event-related desynchrony. Significant mu and beta band ERSPs were found related to the step cycle and were also lateralized depending on the phase of the step cycle and topography. Results suggest it is feasible to record walking related ERD and walking related signals could be used for BCI applications. |
| Yokoyama et al., (2021) | Treadmill walking | Normal walking vs. precision stepping (0.55 m/s) | 13 (range 22–30 years) | 63 | Source | Event-related spectral perturbations, spectral power | Alpha and beta band power decreased, and gamma band power increased in parieto-occipital and sensorimotor cortices during precision stepping compared to normal walking. ERSPs were similar for normal and precision stepping. Results suggest higher cortical involvement and differential roles of brain regions during precision stepping. |
| Zhao et al., (2022) | Treadmill walking | Self-selected speed | 24 (range 22–31 years) | 128 | Source | Event-related spectral perturbations | Gait cycle-related synchronization and desynchronization in alpha, beta, and gamma bands strongest in primary sensorimotor cortex, also found in premotor cortex, thalamus, and cerebellum. Evidence of lateralization in the primary sensorimotor cortex (alpha and beta bands), and in the cerebellum (beta and gamma bands). |
| Jacobsen and Ferris (2023a) | Treadmill walking | Split belt speeds (2:1 ratio, 1.2 m/s and 0.6 m/s) | 33 (mean f: 23.19 ± 2.61, m: 24.22 ± 4.82) | 128 (dual-layer EEG) | Source | Event-related spectral perturbations, spectral power | Multiple cortical regions near the sensorimotor, posterior parietal, and cingulate cortices were found to have alpha and beta band spectral power changes associated with adaptation to split belt speeds. Significant differences in spectral power across stages of gait adaptation during the gait cycle. Results suggest the |

(*continued on next page*)

**Table 2** (*continued*)

| Reference | Task | Manipulation/ Condition | Number of participants (Age) | # EEG sensors (* Denotes invasive sensors) | EEG channel or Source domain analysis | Neural features/ metrics analyzed | Contribution/Major finding |
|---|---|---|---|---|---|---|---|
| | | | | | | | cortex is involved in gait adaptation and with practice the new pattern becomes more automated. |
| Wagner et al., (2012) | Robot assisted walking and upright standing | Low walking speed (1.8–2.2 km/h); active and passive walking | 14 (range 22–28; 24.3 ± 2.7 years) | 120 | Source | Spectral power, event-related spectral perturbations | Evidence of differences in cortical activation between active and passive robot assisted gait. Reduced power in mu and beta bands over central midline areas during active walking could be related to sensory processing of the lower limbs. Cortical activity in the premotor cortex in the lower gamma band, which tended to decrease during active walking, may be related to movement planning and or sensorimotor processing. |
| Lisi and Morimoto, (2015) | Treadmill walking | Volitional gait speed changes between 0, 1, and 2 km/h | 8 (mean 25 ± 2.5 years) | 64 | Source | Event-related spectral perturbations | Mu and beta rhythms suppressed during gait speed changes, suggesting the parietal cortex could be involved in motor planning and visuomotor transformations during gait adjustments. |
| Luu, Brantley, Nakagome, et al., (2017) | Level-ground, ramp ascent, and stair ascent walking | Level-ground, ramp, and stair | 10 (age not provided) | 60 | Source | Spectral power, event-related spectral perturbations | Changes in spectral power in the posterior parietal cortex and sensorimotor cortex were associated with the level of motor task demands. |
| Luu, Brantley, Zhu, et al., (2017) | Level-ground, ramp ascent, and stair ascent walking | Level-ground, ramp, and stair | 6 (age not provided) | 64 | Source | Event-related spectral perturbations | Modulations in posterior parietal cortex shifted to higher frequency bands when ascending stairs and ramps. Low gamma modulations in sensorimotor area observed in level-ground walking shifted to lower frequency bands while ascending stairs and ramps. Suggests that varying walking terrains have distinct neural signatures. |
| Bruijn et al., (2015) | Treadmill walking | Walking normally and with lateral stabilization | 10 (mean 31.4 ± 6.6 years) | 64 | Source | Spectral power | Increased beta power in the left premotor area during stabilized walking suggests a reduced demand to stabilize gait. |
| Sipp et al., (2013) | Treadmill walking | Walking on and off a treadmill-mounted balance beam | 26 (mean 23 ± 5 years) | 256 | Source | Spectral power | Several areas are involved in recognizing a loss of balance, as seen with increased theta band activity before the loss of balance. The first area to show an increase was the sensorimotor cortex, during the last double support phase before stepping off the beam. |
| Peterson and Ferris, (2018) | Walking or standing on a treadmill-mounted balance beam | Physical and visual balance perturbations | 30 (mean 22.5 ± 4.8 years) | 134 | Source | Spectral power, event-related spectral perturbations | Similar time-frequency electrocortical pattern when facing the two types of perturbations, but the pattern was stronger in occipito-parietal areas during visual perturbations |

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**Table 2** (*continued*)

| Reference | Task | Manipulation/ Condition | Number of participants (Age) | # EEG sensors (* Denotes invasive sensors) | EEG channel or Source domain analysis | Neural features/ metrics analyzed | Contribution/Major finding |
|---|---|---|---|---|---|---|---|
| | | | | | | | and stronger in motor areas during physical perturbations. |
| An et al., (2019) | Treadmill walking | Trip perturbation | 5 (mean 24.6 ± 2.0 years) | 128 | Channel | Power spectral density | Alpha band desynchronization during trip recovery in the electrodes over the sensorimotor and posterior parietal cortices during balance recovery suggest increased cortical activity in those areas while recovering walking balance. |
| Wagner et al., (2016) | Treadmill walking | Adaptation to auditory cue pacing | 18 (range 22–35; 29.1 ± 2.7 years) | 108 | Source | Event-related spectral perturbations, event-related potentials | Two beta band oscillatory networks involved in motor adjustments during gait: 1) decrease in mu and beta band reflecting motor execution and readiness related to gait movements; 2) frontal beta band increase related to cognitive top-down control and inhibition. |
| Malcolm et al., (2018) | Treadmill walking | Optic flow with and without continuous mediolateral perturbations, go/no-go task | 16 (mean 25.6 ± 4.5 years) | 72 | Source | Power spectral density | Cautious gait was accompanied by spectral power modulations in frontoparietal clusters, areas that are thought to be involved in motor planning and sensory guidance of movement. Suppression in alpha/mu and beta rhythms suggest increased activation of these regions when sensory inputs are unreliable. |
| Mustile et al., (2021) | Overground walking | Stepping over expected and unexpected obstacles | 32 (range 19–65; 32.1 ± 11.6 years) | 32 | Channel | Event-related spectral perturbations | Changes in frontal theta and centro-parietal beta power before and after obstacle crossing demonstrate distinct neural markers of proactive and reactive movement control. Motor plans are updated as soon as obstacle appears. Beta rebound after obstacle crossing reflects the resetting of the motor system. |
| Nordin et al., (2019) | Treadmill walking and running | Stepping over obstacles | 9 (age not provided) | 128 (dual-layer EEG) | Source | Event-related spectral perturbations | Spectral power increases in supplementary motor area and premotor cortex after the obstacle appeared, but before stepping over the obstacle, suggests these areas prime locomotor control to expect changes to the gait cycle. Spectral power increase in the posterior parietal cortex at a similar distance to contact with the obstacle at each speed suggests its involvement in planning foot placement before stepping over the obstacle. |
| Salazar-Varas et al., (2015) | Treadmill walking | 2 km/h; obstacles (laser projection, change of color of a screen) | 3 (range 24–29 years) | 32 | Channel | Average potential, scalp distribution | Change of potential precedes participants' reaction to obstacle, suggesting a change in |

(*continued on next page*)

**Table 2** (*continued*)

| Reference | Task | Manipulation/ Condition | Number of participants (Age) | # EEG sensors (* Denotes invasive sensors) | EEG channel or Source domain analysis | Neural features/ metrics analyzed | Contribution/Major finding |
|---|---|---|---|---|---|---|---|
| | | | | | | | brain activity reflecting the alertness to the obstacle's appearance and the preparation for a reaction. |
| Jacobsen et al., (2023) | Walking on split-belt treadmill | Adaptation to a 2:1 treadmill belt speed ratio | 30 (mean 22.8 ± 2.6 years) | 128 (dual-layer EEG) | Source | Adaptation time constants for kinematic and electrocortical measures | Electrocortical time constants were larger than kinematic ones, suggesting that adaptive changes in brain dynamics were longer-lasting than the changes in step timing. |
| **Corticocortical and corticomuscular coherence during walking** | | | | | | | |
| Lau et al., (2014) | Standing and walking on a treadmill | Visual oddball discrimination task | 8 (range 20–31 years) | 248 | Source | Cortical connectivity | Stronger connectivity involving sensorimotor clusters in standing than walking, suggesting a greater cortical/cognitive involvement during standing. Connectivities involving non-sensorimotor areas stronger during walking vs. standing only when engaged in the cognitive task. |
| Petersen & Ferris, (2019b) | Standing and walking on a treadmill-mounted balance beam | Physical perturbations and field-of-view rotations. | 30 (mean 22.5 ± 4.8 years) - 1 subject discarded | 136 | Source | Cortical and muscular connectivity, event-related spectral perturbations | Sensorimotor perturbations to balance alter cortical networks. Decreased occipito-parietal connectivity during visual rotations, increased connectivity between supplementary motor and anterior cingulate areas during physical perturbations. |
| Artoni et al., (2017) | Treadmill walking | 3.5 km/h | 11 (mean 30 ± 4 years) | 64 | Source | Corticomuscular connectivity, event-related spectral perturbations (discussed in section on spectral fluctuations of electrocortical activity during walking) | Brain-to-muscle connectivity was stronger than muscle-to-brain connectivity. Motor regions had a stronger influence on leg muscle activity than non-motor regions, suggesting supraspinal involvement in human locomotion. Connectivity was strongest for distal muscles of the swing leg, suggesting fine cortical control for ankle dorsiflexion and foot placement. |
| Brantley et al., (2016) | Overground walking and stair ascent | Level overground walking followed by 8-step stair ascent | 1 (31 years) | 64 | Channel | Corticomuscular coherence | EEG-led corticomuscular coherence during level walking. Coherence increased between EEG and vastus lateralis and tibialis anterior in the delta band during stair ascent. EMG led EEG for biceps femoris and gastrocnemius during stair ascent. |
| Jensen et al., (2018) | Treadmill walking | Visually-guided vs. normal walking | 16 (mean 23 ± 5 years) | 2 | Channel | Corticomuscular, intramuscular, and intermuscular coherence | Increased intramuscular, intermuscular, and corticomuscular coherence (not significant) in ankle dorsiflexors and plantar flexors during visually guided treadmill walking. Suggests that the motor cortex and corticospinal tract are involved in |

(*continued on next page*)

**Table 2** (*continued*)

| Reference | Task | Manipulation/ Condition | Number of participants (Age) | # EEG sensors (* Denotes invasive sensors) | EEG channel or Source domain analysis | Neural features/ metrics analyzed | Contribution/Major finding |
|---|---|---|---|---|---|---|---|
| Jensen et al., (2019) | Treadmill walking | 3.6 km/h | 11 (mean 24.9 ± 2.8 years) | 1 | Channel | Corticomuscular and intermuscular coherence | visually guided foot placement during walking. Significant corticomuscular and intermuscular coherence in beta and gamma bands throughout the stance phase, particularly just before push-off, with EEG activity leading the EMG activity. Suggests that motor cortex contributes to activity in the ankle plantar flexor and to forward propulsion. |
| Petersen et al., (2012) | Treadmill walking | Preferred speed, without active arm swing | 9 (mean 23.4 ± 4.1 years) | 28 | Channel | Corticomuscular coherence | Coupling between EEG (24–40 Hz) over the leg motor area and EMG from the tibialis anterior before heel strike suggests that the motor cortex and corticospinal tract contribute directly to the muscle activity in treadmill walking. |
| Roeder et al., (2018) | Treadmill and overground walking | Preferred speed | 22 (mean 25.9 ± 3.2 years) | 10 | Channel | Event-related power, corticomuscular coherence, intertrial coherence | Cortical power, corticomuscular coherence, and intertrial coherence increased during periods of double support. Frequency-band dependent differences between overground and treadmill walking, suggesting different neural control for the two gait modalities. EEG response preceded the EMG response. |
| Winslow et al., (2016) | Overground walking and ramp ascent | Self-paced | 1 (31 years) | 64 | Channel | Corticomuscular coherence | Activity of the motor cortex led activity in the tibialis anterior in the low gamma band in swing phase during overground walking and in stance phase during ramp ascent. |
| **Invasive EEG** | | | | | | | |
| Starkweather et al., (2023) | Visually cued arm swing and stepping task | Intra-operative seated setup | 5 with idiopathic Parkinson's disease (mean 64.5 ± 10.9 years); 1 with essential tremor (47 years) | 28* (temporary electrode strip over upper limb primary motor cortex in deep brain stimulation patients) | Channel | Spectral power | Oscillatory signatures of stepping were different than those of the arm swing. Oscillations in the hand and arm area of the motor cortex during stepping were in lower frequency ranges (delta, alpha, theta, beta) than the gamma band activity seen during the arm swing. |
| McCrimmon et al., (2018) | Treadmill walking and isolated limb movements | Walking at slow, casual, and fast speeds. Flexion and extension of the hip and knee; ankle dorsiflexion and plantarflexion; isolated arm-swing | 2 (32 and 38 years) | 32* (ECoG grid) | Channel | Spectral power | M1 is involved in high-level gait motor control, encoding walking duration and speed, rather than low-level patterns of leg muscle activation or movement trajectories. |
| Aghajan et al., (2017) | Overground walking | Slow or fast speed, linear and circular paths | 4 (34, 40, 45, and 63 years) | 4* (NeuroPace) | Channel | Spectral power | Theta oscillations observed in rodents were also present in humans but occurred in short bouts that were more prevalent during fast vs. slow movements. |

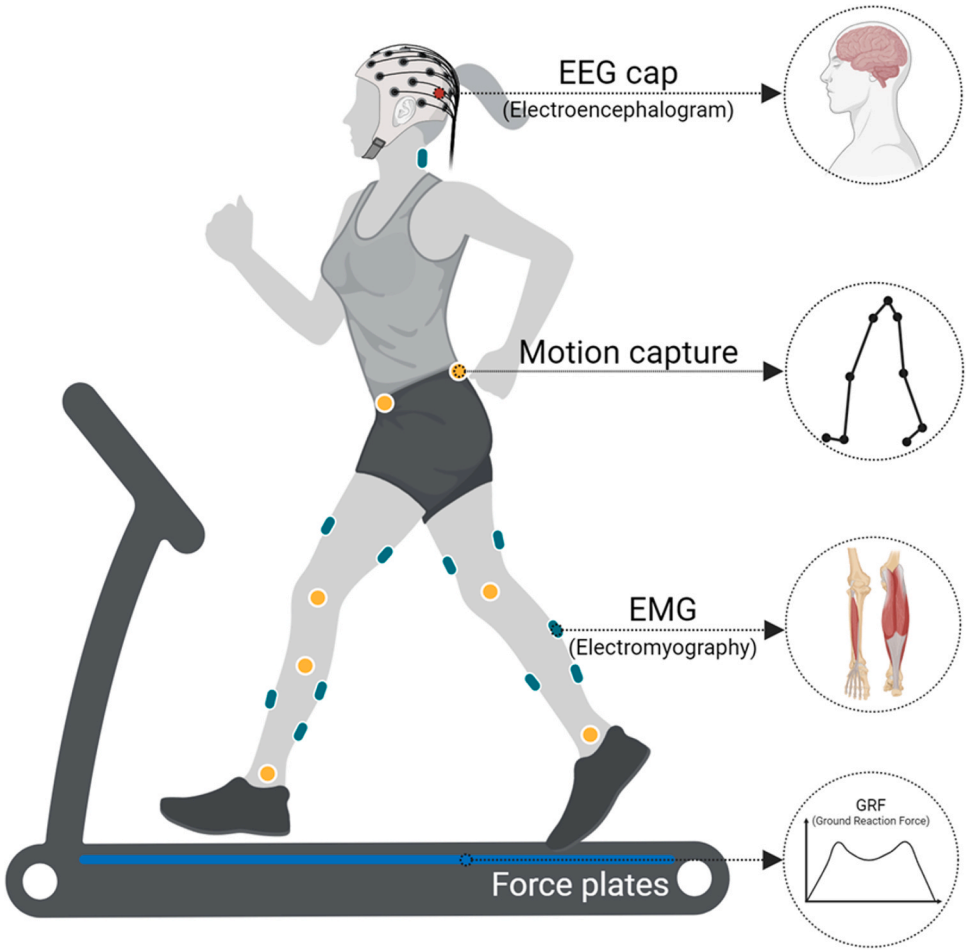


**Fig. 5.** This figure depicts a mobile-brain body imaging (MOBI) experimental setup for studying locomotion-related brain activity in neurologically intact humans. High-density scalp EEG is recorded simultaneously with motion capture, electromyography (EMG), and ground reaction forces (GRF). Measurements of the limb trajectories and muscle activity can help with the interpretation of brain signals and enables analysis such as exploring information flow between brain and muscle. This type of data collection can be performed in the lab on a treadmill, but wireless and portable sensors have enabled the study of locomotion overground and outside of the lab in more realistic, complex settings. (Figure created by Seongmi Song using biorender.com).

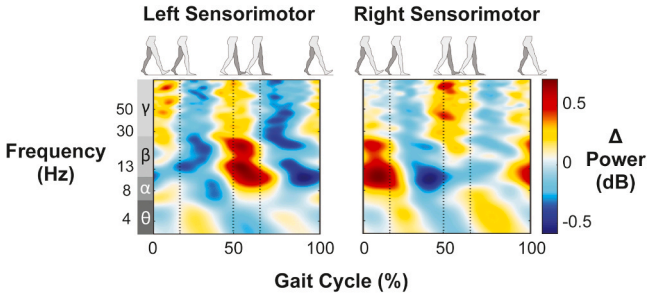


**Fig. 6.** Gait-related spectral perturbation plots from the left and right sensorimotor cortex during normal treadmill walking at 1.2 m/s. These plots illustrate the lateralization of alpha and beta spectral power fluctuations that are typically observed in sensorimotor cortices related to the gait cycle. These plots were created from a split-belt walking study (Jacobsen and Ferris, 2023b). Blue shows decreases in spectral power that occur with desynchronization and red shows increases in spectral power that occur with synchronization. (Figure created by Noelle Jacobsen).

our gait.

Theta synchronization in multiple brain areas is a consistent finding when experiencing gait perturbations. Peterson and Ferris (2018) showed that the type of perturbation, visual or physical, altered the brain areas responding with a robust theta synchronization during walking. With visual perturbations, there was a strong theta synchronization followed by a beta desynchronization in the occipital and posterior parietal cortices. In contrast, physical perturbations showed the same spectral power responses in the anterior cingulate and sensorimotor cortices. An et al. (2019) used a split-belt treadmill to generate unpredictable trip perturbations to walking and observed changes in electrocortical activity in the sensorimotor and posterior parietal cortices while recovering from a trip compared to standing and walking. There was a strong synchronization in the theta band for the sensorimotor cortex and desynchronization in the alpha band for the sensorimotor and posterior parietal cortices during trip recovery. They also found that, in the posterior parietal cortex, theta power increased in walking compared to standing, and that beta power decreased during walking and trip recovery compared to standing. These findings suggest that the type of perturbation used to conduct balance training has a marked effect on what areas of the brain respond for balancing.

Other EEG experiments support the idea that phasic electrocortical activity during walking may reflect processing of sensory information. Walking requires the integration of visual, proprioceptive, cutaneous, and vestibular sensory inputs, which we use to guide our trajectory and to adjust to unexpected events (Peterka, 2018). The brain monitors this feedback to adjust our walking. Studies on gait adaptation demonstrate power fluctuations due to changing sensory cues (Malcolm et al., 2018; Oliveira et al., 2017; Wagner et al., 2016). Wagner et al. (2016) examined gait adaptation to changing pacing cue tones and found beta band

activity modulations in supplementary motor, parietal, and frontal areas following step pacing cue tempo perturbations. Similarly, Malcolm et al. (2018) modified optic flow while walking, which yielded modulations in the supplementary motor area, the anterior cingulate cortex, the inferior parietal lobule, and the precuneus. Closing the eyes during walking has also changed spectral power fluctuations in frontal, premotor and somatosensory cortices (Oliveira et al., 2017). Theta desynchronization was reduced in frontal and premotor cortices during stance and theta to beta desynchronization was increased during single support and right swing phases in left and right sensorimotor cortices. Altogether, the results of these studies suggest that when one sensory modality is not available or inaccurate, sensory reweighting may increase cortical spectral power fluctuations within the gait cycle related to sensory processing and integration of the remaining sensory modalities.

A few experiments have looked at brain activity during obstacle avoidance in human locomotion, and found robust electrocortical signatures (Mustile et al., 2021; Nordin et al., 2019; Salazar-Varas et al., 2015). Salazar-Varas et al. (2015) found a change in potential before participants reacted to an obstacle, suggesting alertness to the obstacle's appearance and preparation for a reaction. Nordin et al. (2019) found increases in spectral power for delta, theta, and alpha bands in supplementary motor area, premotor cortex after participants initially saw an obstacle appear in their path. Later, in the penultimate step before crossing the obstacle, the posterior parietal cortex also showed increases in spectral power. They suggested that the supplementary motor area and premotor cortex prime locomotor control to expect descending modifications to the gait cycle. In contrast, the posterior parietal cortex was likely involved in planning foot placement in anticipation of stepping over the obstacle (Nordin et al., 2019). Mustile et al. (2021) studied avoidance of expected and unexpected obstacles during walking. They found increased frontal theta power when an unexpected obstacle appeared on the path, which was larger when less time and space was available to adjust. The authors suggested this was evidence of proactive control mechanisms in response to unexpected obstacles. They also observed a greater decrease in beta power in sensorimotor areas when obstacles were present, demonstrating increased motor readiness during obstacle avoidance. Participants also had increased parietal beta power after obstacle crossing, evidence of a reactive phase consisting of resetting the motor system to its previous state once the obstacle has been negotiated. These studies suggest multiple cortical areas are involved with identifying and adapting locomotor control to unexpected obstacles. These findings do not always agree with theoretical interpretations from local field potentials in non-human animals (Drew and Marigold, 2015). The main difference in the animal studies is they have used a limited number of brain areas. Future studies on humans with mobile EEG in interactive environments would help provide a more comprehensive view.

Experiments inducing changes in walking pattern indicate major roles for sensorimotor, posterior parietal, and anterior cingulate cortices in controlling gait adaptation. In a recent study of split-belt treadmill adaptation, a common paradigm for studying behavioral metrics in gait adaptation, Jacobsen and Ferris (2023a) found sensorimotor and posterior parietal cortices had decreased alpha and beta band spectral power during early adaptation to split-belt treadmill walking. The spectral power in both areas returned to pre-adaptation levels by the end of the adaptation training period when gait kinematics had stabilized. There were also strong increases in anterior cingulate and posterior cingulate theta band power with the initial gait perturbation of the split-belt treadmill speed differential. When comparing the adaptation time constants for kinematics versus the adaptation time constants for electrocortical measures, the electrocortical time constants were generally longer (Jacobsen et al., 2023). This suggests that the changes in brain dynamics were longer-lasting than the changes in stepping timing. Wagner et al. (2016) used a much shorter duration adjustment in step frequency and length based on an audio tone, but they also found a similar reduction in beta band power for the sensorimotor and posterior parietal cortices. Overall, these observations about gait adaptation are in keeping with the previously discussed observations about gait perturbations and stability.

Several studies, although quite informative about the neural control of balance, are focused on standing balance control and fall outside of the scope of this review. For example, a series of experiments provide insight into cortical dynamics during reactive stepping responses (Ghosn et al., 2020; Solis-Escalante et al., 2019, 2020, 2021; Stokkermans et al., 2022). We would like to refer readers to these recent review papers that offer an excellent summary of the cortical activation in balance control: Huang and Ferris (2023), Payne et al. (2019), Purohit and Bhatt (2022), Varghese et al. (2017), and Wittenberg et al. (2017).

### *Corticocortical and corticomuscular coherence during walking*

The high temporal resolution of EEG makes it an ideal modality for studying connectivity during human locomotion. Lau et al. (2014) found greater effective connectivity between other brain areas and the sensorimotor cortex during standing compared to walking. They interpreted this finding in that standing had greater cortical involvement for control compared to walking. Peterson and Ferris (2019b) reported that effective alpha connectivity between parietal and occipital areas decreased with visual perturbations during walking, and effective theta connectivity between supplementary motor area and sensorimotor, anterior parietal, anterior cingulate, and right occipital areas increased with physical perturbations during walking. Both findings are consistent with theories on sensory re-weighting and error processing.

With inclusion of electromyography measurements, it is possible to combine EEG metrics and EMG metrics to assess corticomuscular coherence during walking (Artoni et al., 2017; Brantley et al., 2016; Jensen et al., 2018, 2019; Petersen et al., 2012; Roeder et al., 2018; Winslow et al., 2016). Corticomuscular coherence can help provide insight into flow of motor commands and sensory feedback from the periphery. Petersen et al. (2012) and Winslow et al. (2016) found coherence between the primary motor cortex and *tibialis anterior* muscle activity in the beta and low gamma bands, as was expected given the strong link between motor cortex and that muscle during gait (Capaday et al., 1999). Artoni et al. (2017) examined the link between brain and muscle including direction of information flow during walking in multiple participants. Brain-to-muscle connectivity was stronger than muscle-to-brain connectivity and motor regions had a stronger causal influence on leg muscle activity than the non-motor regions, demonstrating the supraspinal involvement in human locomotion. They also found that connectivity was strongest for distal muscles of the swing leg, which suggests that cortical control is important for ankle dorsiflexion and correct foot placement. Roeder et al. (2018) examined corticomuscular coherence using bilateral EEG from the sensorimotor cortices and bilateral EMG from the *tibialis anterior*. They found increased corticomuscular coherence during double support at frequencies between 0 and 45 Hz, with EEG signals leading the EMG signals in alpha, beta, and gamma bands. In 2019, Jensen *et al.* recorded EEG with one electrode over the leg motor cortex area and muscle activity of the *medial gastrocnemius* and *soleus* muscles and looked at corticomuscular coherence (Jensen et al., 2019). They found coherence in the beta and gamma frequency bands throughout the stance phase, with EEG activity preceding EMG activity throughout stance and until push-off. They suggest that these findings illustrate the motor cortical contribution to plantar flexor activity in the stance phase of gait and its contribution to forward propulsion during walking.

### *Invasive EEG*

While the previously reported data were acquired through non-invasive methods, there are a few experiments that have evaluated electrocortical locomotor activity using invasive recordings. Starkweather et al. (2023) placed temporary electrode strips over the upper

limb area of the primary motor cortex in deep brain stimulation patients with Parkinson's disease and essential tremor and found different oscillatory signatures between stepping motions and the arm swing. An experiment by McCrimmon et al. (2018) used electrode grids implanted in epileptic patients to examine the human leg area of the primary motor cortex. They provide evidence that the primary motor cortex is involved in the control of walking. They observed a gamma-band synchronization at gait initiation which was maintained during the entire walking bout, indicating that the primary motor cortex is involved not only for gait initiation but throughout the walking duration. Gamma activity also changed across the gait cycle at various walking speeds, suggesting that the primary motor cortex encodes gait speed. Authors note that the gamma-band activity was related to motor intention and not caused by sensory feedback. Interestingly, isolated contraction of ankle and hip muscles did not produce the same electrocortical patterns as walking, suggesting that the primary motor cortex encodes walking duration and speed but not muscle activation patterns or movement trajectories (McCrimmon et al., 2018). It is possible that the primary motor cortex provides rhythmic input to the spinal central pattern generators during walking (McCrimmon et al., 2018).

Other experiments have started to use neurostimulator devices that are implanted for clinical purposes to record intracranial EEG. Similar to the electrode grids, these devices are resistant to motion artifacts, allow access to deep brain structures, and offer the possibility to record data for extended periods of time. They also allow researchers to examine causal relationships between stimulated brain areas and behavior (Stangl et al., 2023). Aghajan et al. (2017) looked at theta-band activity during walking to confirm if theta activity observed in rodents was also present in humans. Walking was done either in a straight line or a circular path at both slow and fast speeds. They found that theta power was significantly higher when participants were in movement compared to when they were immobile and that these oscillations occurred in short bouts that were more prevalent during fast movements (Aghajan et al., 2017). As presented in the overview by Maoz et al. (2023), there are not many studies that have used neurostimulator devices to examine human walking yet, but these methods will enable us to gain valuable information about the electrocortical contributions to walking in natural settings.

### *Next steps in EEG research*

The rapid progress in EEG hardware and processing methods that has occurred over the last decade has led to a plethora of new studies on mobile EEG. Many of the resulting data collections are available freely on various platforms. For example, platforms such as OpenNeuro (https://openneuro.org/) and Nemar (https://nemar.org/) are specific to brain imaging datasets, while other platforms such as IEEEDataPort (https://ieee-dataport.org/) and PhysioNet (https://physionet.org/) offer more general open access datasets. There is therefore a large number of online datasets that can benefit from further analysis from other research groups. Analyzing these data with best practice processing methods and new research questions will yield an even greater understanding of the electrocortical contributions to human walking. In addition, there is a known problem with replication of results in EEG experiments (Pavlov et al., 2021). EEG data are complex and can be preprocessed and analyzed in many different ways, which contributes to this problem. In addition, the complexity and cost of the work can lead to small sample sizes (Pavlov et al., 2021). The online databases that are now available offer us the opportunity to overcome these issues by demonstrating replication of results and ensuring rigor in our data. To help with the problem with replication of results, researchers also need to discuss best practices in the field, which will continue to evolve as new processing methods are developed (Miljevic et al., 2022; Pernet et al., 2020).

Because of the surge of research in mobile EEG, there has been a recent proliferation of available commercial EEG hardware (C. He et al., 2023; Niso et al., 2023). Niso et al. (2023) report on 48 wireless systems, and this number will continue to rise in coming years. Systems vary based on factors such as density and type of electrodes, weight and portability, ease of setup, cost, battery life, real-time access, and additional sensors. Care must be taken when selecting an EEG system, to ensure an adequate signal quality based on the desired application. For mobile EEG research, high-density wireless systems are preferred (C. He et al., 2023). On a positive note, a comparison of two research-grade systems, a mobile system with dry electrodes, and an affordable low-density mobile system has demonstrated that the variability in systems is negligible as long as you use a quality system (Melnik et al., 2017). In addition, there was very little intersession variability, indicating that testing participants only once is sufficient (Melnik et al., 2017).

## Limitations

We have focused the majority of this review on a discussion of the technical approaches and scientific findings of mobile brain imaging with high-density EEG to provide new insight into the control of human locomotion in healthy young adults. There are many other studies focused on clinical populations that we have not discussed, primarily due to the complexity of interpreting data from neurologically impaired individuals. In addition, the effect of aging on the control of human locomotion was not discussed. Another limitation of the review is the lack of discussion on higher order cognition studies, such as those focusing on navigation and social interactions. Those topics have also become popular due to technical advances in mobile EEG, and the increase in research in those areas is likely to continue. Lastly, there are very many studies on mobile EEG that analyze their data in sensor space (i.e., electrode averages) rather than source space (i.e., brain areas), that we have not discussed. It is hard to have great confidence in which brain area is contributing most to a sensor level signal (Makeig et al., 2002, 2004).

## Conclusions

New hardware and signal processing approaches for mobile EEG have greatly expanded our appreciation of the involvement of brain areas in the control of human locomotion. The reasonable spatial resolution and excellent temporal resolution allow source localized electrocortical activity to inform scientists about the tonic and phasic changes in brain activity that correlate with gait speed, stability, perturbations, and adaptation. Perhaps surprisingly, the strong presence of spectral power fluctuations within the anterior cingulate, posterior parietal, occipital, and posterior cingulate areas shows robust results to gait behaviors in addition to the expected presence of spectral power fluctuations within the sensorimotor cortex. The coming years should bring a large increase in controlled experiments that directly manipulate gait parameters and biomechanics to specifically test focused hypotheses on electrocortical activity. We really are just scratching the surface of understanding brain control of human locomotion at this point, but we are very optimistic for the future given the advances in mobile brain imaging technologies.

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