Electroencephalography

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Key points

- Electroencephalography (EEG) is a powerful tool for advancing the fundamental understanding of human brain function.
- Due to the lower cost of this method and its portability, EEG is not only more accessible than other neuroimaging methods, it has a greater potential to translate basic science from the lab to the real world.
- While there are significant clinical applications of EEG, this review is focused on the use of EEG in basic research.
- This review provides a brief historical survey. Given its long history, it is clear that EEG is the first technique for the noninvasive recording of neural activity from the human brain.
- This review briefly summarizes the physiological basis of EEG. Unlike other brain imaging methods used in cognitive neuroscience, EEG is a direct measure of neural activity.
- Two main analytical approaches are summarized: The event-related potential technique and time-frequency methods for analyzing oscillations.
- Two frontiers in EEG research are summarized: Machine learning approaches and mobile brain imaging.

Abstract

The first observations of the human electroencephalogram were made by Hans Berger in the early 1920s. Since that time, this method for the noninvasive recording of human brain activity has led to a number of foundational discoveries about human information processing and has become an important tool for cognitive neuroscientists. This review is divided into four main sections that provide the reader with some historical context, information about the physiological basis of the EEG signal, foundational methodological approaches using EEG data to inform our understanding of human brain function, and recent advances and frontiers.

Introduction and scope

A complete understanding of typical and atypical cognitive function in the lab and in the real world requires precise noninvasive measurements of brain activity. The first observations of the human electroencephalogram were recorded in the 1920s, over 60 years prior to the first reports using functional magnetic resonance imaging (fMRI) of the human brain without contrast injections (Ogawa et al., 1990). As a result, electroencephalography (EEG) is the first method for the noninvasive recording of human brain activity. EEG is a direct measure of neural activity, has exquisite temporal resolution, and is relatively low-cost, all in contrast to fMRI. One of the interesting aspects of EEG that makes it an especially appealing signal of brain activity to use to inform theory is that different features of the signal carry important information about sensory, perceptual, and cognitive functions. As a result of these characteristics, EEG has wide clinical applications, has been a key tool for informing mechanistic theories of cognitive function, and, more recently, has become an important tool for translating basic scientific discoveries to real-world applications outside the lab.

In this article, we first provide a brief historical summary of the origins of EEG research, the physiological basis of the signal, and basic principles of recording. Then, two approaches to characterizing the EEG signal that have been widely employed to address fundamental questions about human cognition and performance will be discussed: event-related potentials and oscillations. Finally, two frontiers in EEG research will be summarized: machine learning methods and mobile brain imaging. Throughout this article, the emphasis will be on basic (i.e., non-clinical) scalp-recorded human EEG studies.

History

The first recorded electroencephalogram was made by Caton (1875). These initial recordings were made in nonhuman mammals and they were invasive recordings, involving electrodes placed directly on the cortical surface. Even though Caton characterized the electrical currents as “feeble”, in his estimation they were directly related to the functioning of the gray matter and modulated by light stimulation. The first report of the human EEG was published by Berger (1929), but the recordings themselves occurred in 1924. In his initial report, Berger cited Caton’s work, suggesting that the previous work in animals served as inspiration for Berger’s explorations to discover the human electroencephalogram. Like Caton’s recordings, Berger’s initial protocol was invasive, with the electrode being placed not only under the scalp, but under the periosteum (the inner layer of the dura mater). Berger soon thereafter developed a noninvasive protocol for placing electrodes on the scalp.

Berger described several key features of the first recording that are hallmarks of the human EEG. The one most commonly referred to is the alpha rhythm, a spontaneous oscillation that occurred at a frequency of about 10 Hz and that increased in amplitude when the eyes were closed compared to when the eyes were open (see Fig. 1). Berger also noted that when a person is in a higher arousal state (e.g., eyes open, engaged in a task) the alpha wave was suppressed, and revealed the presence of faster oscillations that Berger denoted as beta waves.

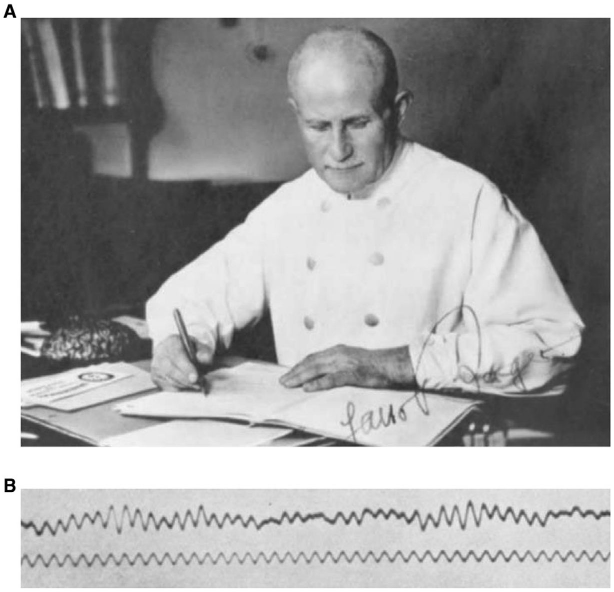

Fig. 1 (A) Hans Berger. (B) One of Berger’s original recordings from his son Klaus. Top line is an EEG trace showing the alpha rhythm. Bottom line is a time reference waveform cycling at 0.1 s. (A) Photo from: Stone and Hughes (2013); (B) From Figure 13 in: Berger (1929).

Berger's initial reports on the alpha rhythm were met with skepticism. There was concern expressed in the literature that the alpha rhythm was nothing more than noise (for reviews see: Başar, 1980; Karakaş and Barry, 2017). Even Berger himself expressed concern about the source of the brain waves in his original report. American scientists Adrian and Matthews (1934) set out to demonstrate that the so-called Berger rhythm was, indeed, an artifact. However, instead of disconfirming the validity of Berger's report, through a series of manipulations of state and exposure to sensory stimuli, Adrian and Matthews confirmed Berger's observations and concluded that the voltage fluctuations were originating from the brain. The reader is referred to Stone and Hughes (2013) for a thorough review of the early history of EEG.

Physiological basis

While EEG is a direct measure of neural activity, it does not measure action potentials. The current understanding of the source of EEG is that it is primarily driven by large scale voltage fluctuations that are the result of synchronous post-synaptic neural activity. After an action potential is evoked, neurotransmitters are released into the post-synaptic cleft. When those neurotransmitters bind onto the post-synaptic neuron, there is a change in charge across the body of the neuron. To balance this charge, there is a passive outflow of ions at the apical dendrites. The net result is a large scale-voltage differential across the cell.

When measuring EEG, the observed changes in potential over time are not caused by single neurons or a small group, but rather large neural assemblies that are similarly oriented and firing synchronously (e.g., Murakami and Okada, 2006). The dependence on geometry and synchronous firing has led to the implication that pyramidal neurons are thought to be the primary drivers of the EEG signal. Pyramidal neurons are present in the neocortex and in subcortical structures. Neocortical pyramidal neurons in particular are an abundant class of excitatory neurons in cortex that are organized perpendicular to the cortical sheath. In addition, pyramidal neurons (typically) span multiple layers of cortex, including layer III and IV, with the cell bodies and basal dendrites located in deeper layers and the apical dendrites in superficial layers (for a primer on pyramidal neurons see: Bekkers, 2011). The perpendicular arrangement creates so-called "open electrical fields" that sum in strength.

There is shockingly little direct evidence for the hypothesis that pyramidal neurons are the primary driver of the EEG signal, but there is some. For example, simultaneous laminar and surface event-related potential recordings in non-human primates have revealed fluctuations in the current source density across cortical layers in visual areas, as would be expected from pyramidal neurons spanning multiple layers of cortex (Mehta et al., 2000a,b). Subcortical contributions to the EEG are thought to be minimal because the pyramidal neurons in those structures do not have the consistent perpendicular arrangement (i.e., they create "closed fields").

The voltage differentials caused by pyramidal neurons can be measured remotely by electrodes placed on the scalp. There are a number of biophysical properties and constraints that influence the remote recording of the EEG signal (for a thorough treatment of the biophysics of EEG, the reader is encouraged to consult Nunez and Srinivasan (2006)). The remote sensing of local neural activity is possible because the skull is a volume conductor. Each tissue between the activated population and the sensor (e.g., gray matter, white matter, CSF, dura, bone, muscle, skin) has different impedance properties that serve to smear the signal in space and time. Nevertheless, the potentials caused by neural activity sum and are conducted to the scalp at the speed of light via the path of least resistance. Given the skull's volume conducting properties, electrodes on the scalp are sensitive to activity from proximal sources as well as distal sources. In addition, the electrodes are also sensitive to other forms of noise, including those that are biophysical (EMG, skin conductance) and those that are not (e.g., ambient electromagnetic fields present in the environment, physical movement). These contaminants place a strong emphasis on creating an electrically quiet recording environment, tight experimental control holding contribution of other sources constant, and the ability to keep participants comfortable and still.

The biophysical principles that allow researchers and clinicians to record EEG noninvasively from the scalp also place important constraints on understanding the signal itself. Three of these principles are essential for understanding the utility of EEG in cognitive neuroscience. First, the polarity measured at the scalp depends on a number of factors including neurotransmitter type, synapse location, orientation of the cortical surface, and the superposition of other sources of electrical activity (brain or non-brain). Second, the absolute amplitude measured at the scalp depends on the number of neurons activated, the geometry of the neurons, the synchronicity of the post-synaptic potentials, the depth of the source, the orientation of the cortical surface, and superposition of other sources. Third, the signal measured at any given scalp location could be produced by an infinite number of possible combinations of cortical sources and, as a result, the localization of specific cortical sources based on scalp-recorded activity alone is an ill-posed problem. The implications of these constraints are that there is nothing inherently special about polarity or amplitude as they relate cognitive function, and inferring specific cortical generators of the EEG based on scalp-recorded activity alone is a risky proposition (for a detailed discussion of these implications and more see: Luck, 2014). This is not to say that the scalp recorded activity cannot be localized, indeed, there are several well-established methods for doing so, including dipole source localization (Scherg, 1992), multiple source beamforming (Gross et al., 2001), and integration with neuroimaging data acquired simultaneously (Herrmann and Debener, 2008) or in separate sessions (Heinze et al., 1994; Mangun et al., 1998; Martínez et al., 1999).

Recording

The basic principles of EEG recording remained largely unchanged from Berger's original noninvasive recording until the end of the 20th century. Recording EEG requires electrically conductive electrodes and an amplifier of some form. A minimum of three electrodes are required: a ground electrode, a reference electrode, and an "active" electrode. The traditional amplifier is set-up in the form of a differential amplifier, where the difference between the voltage at the active-ground connection and reference-ground connection gets amplified. The biggest change between Berger's time and the end of the 20th century was in how the analog signal was stored (e.g., paper, tape, digital) and ultimately how the analog signal was converted to a digital one.

In the last 20 years there has been fundamental changes in electronics that have paved the way for changes in the recording set-ups. Perhaps one of the biggest changes has been the popularization of recording systems that use the driven-right leg design (Winter and Webster, 1983) coupled with active amplification at each electrode (e.g., Biosemi, Netherlands; Brain Products, Germany). The key aspect of the driven-right leg design is that a very small amount of current is applied to the scalp and then sensed by a dedicated electrode. The applied current is intended to ensure that the ground level of the recording is optimal for the common mode rejection of the differential amplifiers. In two popular research systems (ActiveTwo, BioSemi; actiCHamp, Brain Products), there are two amplification stages, one at each electrode and one at the head box. With advances in electronics, the amplifiers have a much broader dynamic range. Traditional amplifiers would "saturate" rendering the signal meaningless if there was too much noise in the recording, but modern amplifiers can tolerate much larger ranges in the signal. A second important change is the advances and availability of new chip design (e.g., solid state memory), which have both reduced the size and cost of modern recording systems. This has meant that EEG has become more accessible to a broader range of researchers, it has made it more mobile, and while there is no substitute for clean data, these advances in circuit design and amplification have meant that it is possible to make clean recordings in a wider range of environmental settings.

Empirical applications to understanding cognition

EEG has been a powerful tool used to understand the foundational mechanisms of human cognition. The promise of EEG was recognized in 1938 by Woodworth who, in the first edition of his classic Psychology text book suggested "We may be able in the future to use 'brain waves' as indicators of the beginning and end of mental processes, …" (p. 288, Woodworth, 1938). In the first few decades after Berger's observations, there was relatively limited application of EEG, likely influenced by a combination of methodological challenges and world events (i.e., World War II). It really wasn't until the 1960s and early 70s when EEG became a more commonly used method for informing human cognition. The method is now a cornerstone of cognitive neuroscience and its popularity has continued to grow. In the past 20 years, there has been a fourfold increase in the annual number of publications that mention EEG (**Fig. 2**). In this section, we will provide a brief summary of the two main methods for characterizing the EEG that have been used to study the basic mechanisms of cognition: The event-related potential (ERP) technique and oscillations. Given the

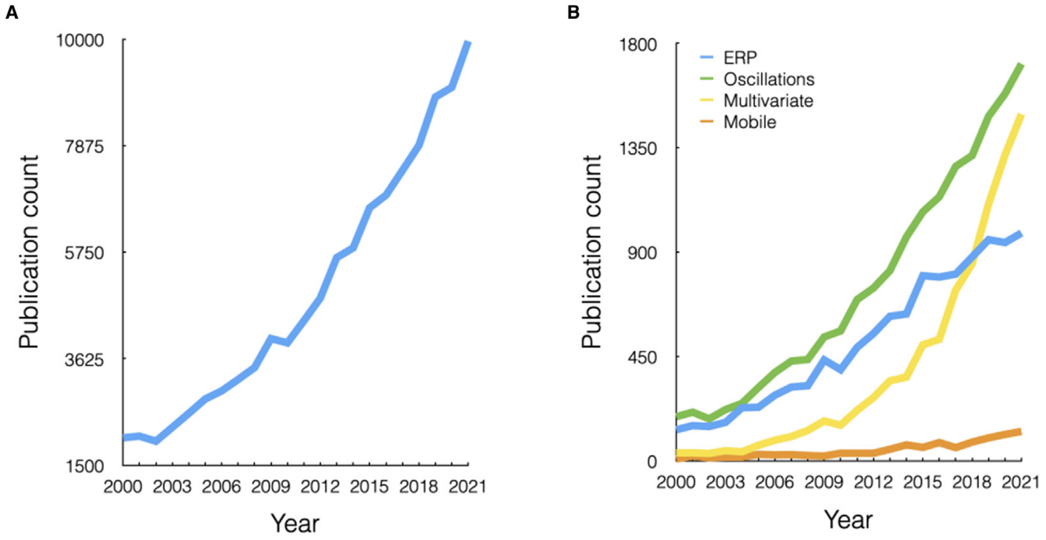

Fig. 2 EEG publication trends from 2000 to 2021. (A) Annual number of EEG publications. Search conducted using the Web of Science database with the following syntax: TS = (EEG or electroencephalography). (B) Annual number of EEG publications in four topic areas relevant for the present review. Searches conducted using the Web of Science database with the following syntax: ERP: TS = (EEG or electroencephalography) and (event-related potentials or ERP); Oscillations: TS = (EEG or electroencephalography) and (oscillations or time frequency analysis); Multivariate: TS = (EEG or electroencephalography) and (pattern classification or decoding or machine learning); Mobile: TS = (EEG or electroencephalography) and (mobile brain imaging or ambulatory or locomotion).

volume of work using EEG in general and the volume of work that has used ERPs and oscillations (**Fig. 2**), this review is not intended to be exhaustive, but rather is intended to capture both historical highlights and noteworthy recent trends.

The event-related potential technique

In any task, the ongoing EEG activity includes responses that are associated with task-related stimulus events, internal task-related mental events, task-related motor activity, task-unrelated sources of brain activity, and other sources of biophysical, physical, and electromagnetic noise. Relative to the amplitude of the summed activity of all these sources, the amplitude of the task-related responses is small and, in most cases, responses to single events are obscured by noise. If the sources of task-unrelated activity and noise are independent of the task-related activity, then averaging the response to multiple events of the same type (e.g., a specific stimulus or experimental condition), will result in the cancellation of the noise from the averaged signal. The event-related response to a specific event (single trial or averaged) is a series of voltage deflections over time that are specific to the event, typically labeled using their polarity (e.g., positive = P; negative = N) and ordinal position in time (e.g., the first positive deflection = P1). These deflections can be quantified in terms of their amplitude and latency. The deflections are thought to characterize the activity of one or more underlying neural computations, or components, that are not directly observable. The distinction between the peaks and troughs in the averaged signal and the underlying contributing components is an important one to make, but is often overlooked in the literature (Luck, 2014; Woodman, 2010). This caveat notwithstanding, the approach of quantifying the response to single events or averaging responses to unique events is at the heart of the event-related potential (ERP) technique. It requires precise temporal records of events, synchronization of these event records with the acquisition of the EEG data, strong experimental design, clean recordings, and, in many situations, large numbers of trials per experimental condition (e.g., ~100). When implemented well, this technique has proven to be a powerful tool for understanding the neural mechanisms of cognition.

Pauline Davis (1939) is typically credited with the first published account using the event-related approach. In her groundbreaking studies, observers heard clicks of various frequencies. She observed that although not all auditory stimuli evoked a response under all conditions, when there was a response, it consisted of several fluctuations that were strongest at the vertex location (Cz in the 10–20 electrode placement system, Jasper, 1958). Ruth Cruikshank (1937) authored one of the earliest reports of the visually evoked response from scalp recordings in humans. She characterized the suppression of the Berger rhythm in response to visual stimulation and the modulation of the evoked potential as a function of stimulus intensity.

The initial reports of event-related responses were really focused on understanding the fundamental properties of the sensory evoked neural activity. It wasn't until after the development of the first signal averaging methods (Dawson, 1954), that it became more common to relate the averaged event-related responses to different cognitive and motor states and test hypotheses about human information processing. One landmark study was the discovery of the contingent negative variation (CNV) by Walter et al. (1964). In this experiment, participants were presented with pairs of stimuli, sequentially, and each required a speeded response. The time between the two stimuli was fixed at 1 s. Walter et al. (1964) observed that between the stimuli, there was a slow negative wave that ramped negatively until the response was made. This negative wave was present only when there was the requirement to respond to the second stimulus and that stimulus was expected. Kornhuber and Deecke (1965) characterized a different type of evoked response prior to voluntary movements at precentral electrodes contralateral to the responding effector. This negative-going deflection is also known as the lateralized readiness potential or the *bereitschaftspotential*.

In another classic study from the same time period, Sutton et al. (1965) presented participants with pairs of stimuli (auditory or visual) sequentially. On some trials, the first stimulus provided the participant with some certainty about the quality or modality of the second stimulus, in effect, acting like a cue. In the instance when the first stimulus provided information about the modality of the second stimulus, participants were asked to make a judgment about the modality of the next stimulus. On some trials, the second stimulus matched the cue-generated expectation and on some trials it did not. Over occipital and parietal electrodes, there was a prominent positive deflection in the averaged response occurring at about 300 ms post-stimulus on uncertain trials compared to certain trials. This response is what we now know as the P3, or P300, ERP component and it is perhaps the most studied ERP component in the literature due to its robustness and tight association with the time course of information processing (Donchin, 1981; Kutas et al., 1977; Polich, 2007).

Aside from the discovery of individual ERP components associated with human information processing, the ERP technique has been proven to be a powerful tool for informing our theoretical understanding of cognition. An excellent example of the theoretical utility of the ERP technique is a body of work conducted by Steve Hillyard and his colleagues addressing fundamental questions about human attention. For example, in the 1960s there was growing debate about whether selective attention operated at early stages of information processing, well before semantic representations were extracted (e.g., Broadbent, 1958; Cherry, 1953), or at later stages of information processing, after higher level (e.g., categorical/semantic) processing was complete (e.g., Deutsch and Deutsch, 1963; Moray, 1959). Hillyard et al. (1973) used the ERP technique to inform this debate. Participants were presented tone pips to either the left ear or right ear and, in different blocks of trials, they were instructed to attend to either the left ear or the right ear for a rare target pip that was a different frequency than most of the other pips. When the responses to the attended and unattended stimuli were compared, Hillyard showed selective attention increased the amplitude of the auditory evoked response within about 150 ms of the presentation of a stimulus. This result was the first demonstration that selective attention could not only modulate brain activity evoked by environmental stimuli, but it demonstrated that selective attention could operate at a very early stage of information processing. Van Voorhis and Hillyard (1977) subsequently demonstrated that visual selective attention to specific locations can modulate the evoked response to stimuli presented in that location. Hillyard and Münte (1984) further demonstrated that just as attending to spatial locations can modulate evoked responses to stimuli, attending to nonspatial stimulus features, like color, can also modulate evoked responses. Mangun and Hillyard (1990) showed that these effects of attention on visual responses are not contingent on sustained attention to a particular location over a block of trials, but rather can be observed when the attended location is cued probabilistically on a trial-to-trial basis.

In addition to contributing to the understanding of motor-related processes and selective attention, the ERP technique has informed our understanding of the full scope of human information processing. For example, when participants are presented images of faces and nonface objects, there is a negative response at lateral occipital electrodes occurring 170 ms post-stimulus that is larger for faces than objects (Bentin et al., 1996). This ERP has been labeled as the N170 and subsequent work demonstrated that its amplitude is modulated by face inversion, consistent with the notion that it is a selective response tied to face perception (Rossion, 1999). In visual search tasks, when a target is presented among a number of distracting items, there is a positive going deflection on the N2 ERP component at posterior electrodes contralateral to the target stimulus (Luck and Hillyard, 1994). This response, labeled the N2pc, is thought to support the selection of the target through a combination of enhancement of the target and suppression of the surrounding distractors (e.g., Eimer, 1996; Kiss et al., 2008; Woodman et al., 2009). Focusing on later stages of processing, Kutas and Hillyard (1980) used the event-related potential technique to characterize the timing of semantic processing in word and sentence reading. In those studies participants read 7-word sentences in which the last word of the sentence either matched or mismatched the context established by the sentence. On trials in which there was a mismatch, there was a large negative going deflection in the evoked response to the word that occurred starting around 300 ms and peaking at about 400 ms post-stimulus. This response was labeled the N400 and its timing, polarity, distribution and insensitivity to physical stimulus manipulations dissociated this response from other possible responses (e.g., N2 or P3). For a more comprehensive summary of the historical applications of the ERP technique in the 20th century, the interested reader is encouraged to refer to Steve Luck's introduction to the technique (Luck, 2014).

In the past two decades, the application of the ERP technique has continued to grow, although this activity has leveled off in the past several years relative to other topics (**Fig. 2**B). Nevertheless, there have been several important discoveries of new ERP components associated with human cognition. For example, Vogel and Machizawa (2004) presented participants with a visual working memory task. Each trial began with a cue that indicated the side of the display that was to be remembered. After a brief delay, an array of colored squares was presented briefly and participants were asked to remember the display over a brief retention period. At the end of the trial, they were presented with another array that was either the same as the original display or was different (i.e., one square changed colors). Vogel and Machizawa observed a large deflection in the event-related response starting at about 300 ms after the first array was presented, during the retention period. This deflection was more negative at posterior electrode sites contralateral to the to-be-remembered items. The amplitude of the difference between contralateral and ipsilateral responses is referred to as the contralateral delay activity (CDA). The CDA increased with the number of items held in working memory and the amplitude appeared to hit a ceiling when the displays were at about the typical working memory capacity of 3–4 items. Importantly, the amplitude of the CDA was correlated with individual differences in working memory capacity. In a subsequent study, Vogel et al. (2005) used the CDA to demonstrate that individuals with high working memory capacity are better able to control what gets in to working memory in the first place, suggesting that an individual's working memory capacity may reflect a combination of both how much one can store, but also the efficiency with which one selects information to store.

A second important finding has been the discovery of an ERP component associated with the suppression of distractors during visual search (Hickey et al., 2009). This component, labeled the distractor positivity (Pd), was discovered using a novel modification of a visual search task that had been used to reveal the N2pc (e.g., Luck and Hillyard, 1994) that involved lateralizing the distractor stimulus and positioning target on the vertical meridian of the display. The logic was that placing the target on the vertical meridian would effectively remove the lateralized N2pc activity evoked by the target. Hickey et al. (2009) observed evidence for the suppression of the cortical representation of the distractor as indexed by the lateralized response. This finding has led to the notion that attention acts to both enhance task-relevant target representations and suppress distractor sensory representations and each of these mechanisms can be measured with EEG (e.g., Sawaki et al., 2012).

Finally, the ERP technique has been used to inform cognition in a variety of tasks, but these tasks typically require that participants remain fixated in order to avoid large ocular artifacts caused by eye movements. However, forced fixation is not a typical condition of natural viewing, which has limited generalizing the results of ERP experiments to real-world tasks (e.g., reading and search). To address this issue, Baccino and Manuta (2005) described methods for synchronizing eye position measured with an infrared eye tracker and EEG evoked response in a reading task. This approach has been used in a variety of experimental contexts besides reading (e.g., visual search, Ries et al., 2016). There have been also been variety of analytical enhancements to this approach (e.g., Cornelissen et al., 2019). As a result, fixation related ERPs represent an important tool for informing human cognition and bridging between tightly controlled laboratory conditions and real-world tasks.

Oscillations

Population level neural activity is highly variable over time, even in the absence of external events. This activity is oscillatory in nature and arises from interactions between the dynamics of various biophysical mechanisms such as excitatory-inhibitory loops, gated membrane channels, and intermittent action potentials (Wang, 2010). Oscillatory activity is a prominent feature in the EEG signal that can be observed at multiple temporal and spatial scales (Cohen, 2017). These brain waves are examined through time-frequency analysis, which relies on spectral decomposition of the recorded signal to extract measurements of power (i.e., squared amplitude) and phase for individual frequencies. The most widely used spectral decomposition methods are the Fourier, wavelet, and Hilbert transforms. These methods yield similar results but differ slightly in their frequency and temporal resolution (Cohen, 2014a). Once spectral properties have been extracted from the signal, EEG oscillations are typically grouped into the following frequency bands (Hz): delta (<4), theta (4–7), alpha (8–12), beta (13–30), and gamma (>30). The cognitive relevance and inferred neural computations of activity within a frequency band are contingent on their cortical generators and the context in which they were recorded (Cohen, 2017). For example, alpha band activity over motor cortex is associated with a different cognitive process compared to the same activity observed over visual cortex (Luck, 2014). Importantly, neural oscillations reflect the coordination of information processing across multiple brain regions.

Early work on the existence and functional role of neural oscillations primarily focused on alpha band activity. As summarized in **History** section, Berger (1929) was the first to report the presence of an alpha oscillation over occipital areas during a low arousal state. He also observed the emergence of the beta oscillation when alpha was suppressed. Improving on the designs of Berger's machine, Walter (1936) found that delta waves could be used to localize intracranial tumors. A series of elegant studies by Adrian and Matthews (1934) and Cruikshank (1937) demonstrated the sensitivity of these oscillations to external events.

Much like the literature on evoked responses, the nature of EEG oscillations received little attention after their initial discovery until around the 1960s. Advancements in recording technology and the development of computerized analysis methods, such as the revolutionary fast Fourier transform (FFT) (Cooley and Tukey, 1965), facilitated the subsequent rise in EEG oscillation research. Much of this research was led by Erol Başar, who systematically explored the dynamics of neural oscillations across multiple biophysical systems (Başar, 1998). Through extensive study of gamma and delta waves, Başar demonstrated that EEG reflected the activity of an ensemble of neural generators that oscillated randomly and spontaneously. These generators are synchronized in response to sensory stimulation, giving rise to evoked potentials. Importantly, Başar revealed that oscillations reflected neural codes of information processing, which laid the foundation for the study of event-related activity in the time-frequency domain.

Contemporary EEG research has focused on establishing the cognitive relevance of canonical frequency bands. The most widely studied oscillations are those within the alpha-band that are localized over visual cortex. Alpha is postulated to reflect inhibitory mechanisms that improve stimulus processing signal-to-noise ratio (SNR) (Haegens et al., 2011; Jensen and Mazaheri, 2010; Palva and Palva, 2007). This notion is supported by the classic finding that alpha power is larger over the ipsilateral versus contralateral hemisphere in response to a cued stimulus in the contralateral hemifield (Medendorp et al., 2007; Thut et al., 2006; Worden et al., 2000), suggesting that alpha is related to the suppression of task irrelevant information (Kelly et al., 2006; Klimesch, 2012; but see Foster and Awh, 2019). Based on these characteristics, alpha-band activity has been linked to spatial attention, but there is also evidence that pre-stimulus alpha-band activity predicts performance on sustained attention (e.g., O'Connell et al., 2009) and nonspatial discrimination tasks, implying that alpha activity also reflects anticipatory attention (Hanslmayr et al., 2007) that can wax and wane over time. Research on the attentional blink (AB) phenomenon, which is the reduced ability to report a second target (T2) presented 200–500 ms after a preceding target (T1), has shown that the magnitude of the AB effect is dependent on alpha phase at T2 onset. When alpha phase is at a certain angle, the amplitude of the P1 component in response to T2 is drastically diminished (Mathewson et al., 2009; Zauner et al., 2012). In addition, the topographic distribution of alpha power tracks the allocation of visuospatial attention toward both external stimuli and active working memory (WM) representations (Foster et al., 2016; MacLean et al., 2019; Samaha et al., 2016; Sauseng et al., 2005; Sutterer et al., 2019; Thut et al., 2006). Taken together, these findings support the idea that alpha reflects both the suppressive and selective components of attention (Foster and Awh, 2019).

Two other popular sets of oscillations are theta and motor system beta. Frontal midline (Fm) theta waves are generated in the anterior cingulate cortex and are hypothesized to coordinate the transfer of information across networks dependent on midfrontal areas (Cavanagh and Frank, 2014; Cohen, 2014b). Theta power is also modulated in response to cues prior to the presentation of attended stimuli (Green and McDonald, 2008) and in a variety of working memory tasks (for a review see: de Vries et al., 2020). Considering that activity within this band is sensitive to response inhibition, memory encoding and retrieval, working memory maintenance, and cognitive effort, it is thought to reflect a common mechanism for implementing cognitive control in tasks with a high degree of uncertainty (Cavanagh et al., 2009; Cavanagh and Frank, 2014).

Oscillations within the beta frequency range have been tied to volitional movement. Beta waves are prominent in the somatomotor cortex, cerebellar system, and basal ganglia. The level of beta activity is inversely related to the anticipation of executing a voluntary movement, where beta power decreases as evidence accumulates to make a response on a perceptual decision task. In contrast, beta power increases when a cue indicates that a motor response must be suppressed (see Jenkinson and Brown, 2011 for review). Furthermore, there is evidence that the suppression of beta activity correlates with reaction time (Senkowski et al., 2006).

Gamma oscillations are selectively distributed across multiple cortical and subcortical areas, and are modulated by perception, working memory, motor control, and attention based tasks (Jensen et al., 2007; Tallon-Baudry and Bertrand, 1999). Thus, it has been difficult to ascribe a function to oscillations within this wide frequency band (Cohen, 2017). This is especially true in EEG research since the skull acts as a low pass filter that can distort high-frequency gamma. The current leading hypothesis is that gamma activity plays a role in the construction of stimulus representations (Başar, 2013; Gray and Singer, 1989). For example, gamma power increases in response to coherent versus non-coherent visual stimuli (Tallon-Baudry and Bertrand, 1999). Power also increases when individuals report perceiving an object within a noisy display, irrespective of whether or not the object is actually present. This suggests that gamma reflects the construction of percepts through both top-down and bottom-up mechanisms.

Delta oscillations, the slowest frequency band, are prominent during non-rapid eye movement (NREM) sleep. Also known as slow waves, these oscillations are thought to mediate homeostatic processes during sleep and can be used as an index of sleep need (Bellesi et al., 2014). During sleep, slow wave activity selectively increases in brain regions engaged during the completion of a prior learning task. Therefore, slow waves may play a critical role in the consolidation of previous learned associations into long-term memory.

Despite the great strides that have been made toward characterizing EEG oscillations, there remain open questions regarding their dynamics. For example, prior work on neural oscillations has predominantly focused on the link between periodic activity and cognition. Yet, the prevalent aperiodic activity that coexists with these oscillations has received little attention (Cole and Voytek, 2019; Donoghue et al., 2020). This aperiodic component can be observed in the power spectrum of EEG data and follows a $1/f$ distribution with exponentially decreasing power as frequency increases. Examining modulations in canonical frequency bands without considering this component can lead to false conclusions (Donoghue et al., 2020). For instance, modulation of narrow-band activity may reflect a shift in the distribution of aperiodic power rather than between group/condition differences in power. Typically, this component has been treated as noise, but there is emerging evidence that it has physiological relevance and is linked to cognition. Indeed, alterations of the aperiodic exponent has been shown to underlie age-related differences in oscillatory power, and event-related changes in aperiodic activity is predictive of individual working memory performance (Donoghue et al., 2020). Additionally, although neural activity is nonstationary and nonsinusoidal, popular spectral decomposition algorithms model the recorded signal as a combination of stationary sinusoids. This can lead to over-simplified or artifactual account on the function of an oscillation (Cole and Voytek, 2019).

The special case of the steady state visually evoked potential

When Adrian and Matthews (1934) conducted their initial investigations of the Berger rhythm, they included experiments in which a uniform visual field flickered at specific frequencies. They observed that the resulting EEG waveforms carried rhythms of the same frequency as the flashing visual stimuli. Over the years there have been repeated demonstrations that the sustained, rapid, sequential presentation of visual stimuli at fixed frequencies can induce oscillations in the ongoing EEG, the power of which peaks at the specific stimulation frequencies and some harmonics (Regan, 1989). In other words, it is an oscillation, but one that is tied to a specific train of stimulus events. For example, consider the experiment shown in **Fig. 3**. Participants were presented with a 3 s sequence of oriented gratings, flickering at 15 Hz. Sometime between 2 and 3 s, the grating turned clockwise or counter clockwise and the participant was required to indicate the direction of the turn. If one performs a FFT on the EEG data acquired before the grating rotated, there is a clear spike at the stimulus driving frequency of 15 Hz and the peak amplitude is highest at occipital electrode sites. This peak response is the steady state visually evoked potential (SSVEP).

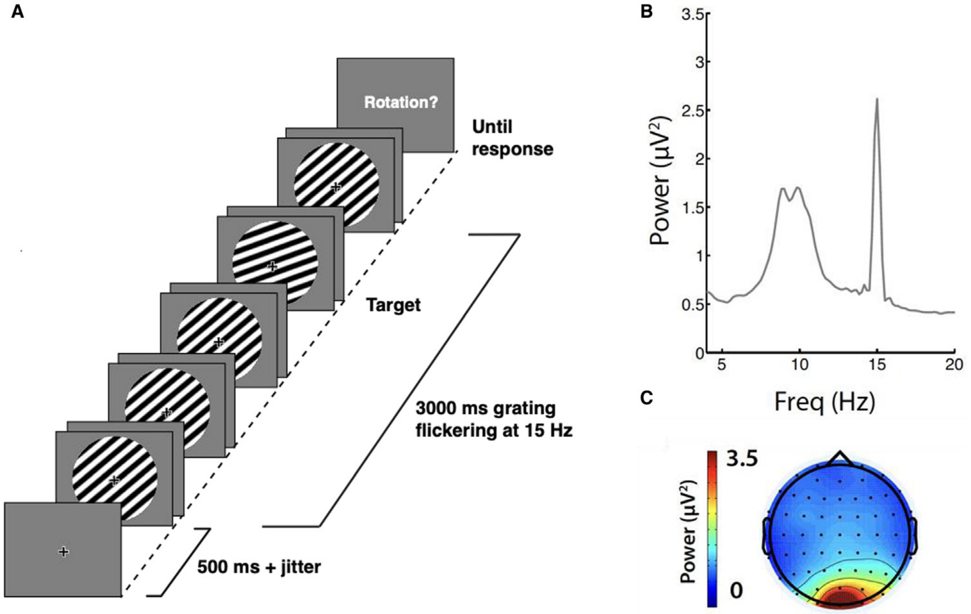

Fig. 3 Example of the Steady State Visually Evoked Potential (SSVEP). (A) Sample task involving the presentation of oriented grating flickering at 15 Hz. Stimulus flickers for 3 s, sometime between 2 and 3 s the grating rotates left or right. (B) Spectrogram showing the results of an FFT conducted prior to stimulus rotation. Spectrogram shows a clear spike in power at the stimulation frequency (15 Hz). (C) Topographic plot showing the scalp distribution of power at the stimulation frequency. The amplitude is highest at occipital electrodes. Task and data were published in Bullock et al. (2017).

The nature of the stimuli used to induce the steady state visually evoked potential (SSVEP) alters the amplitude of the response and the specific frequency of maximal power (i.e., the fundamental stimulation frequency or one of the harmonics). The SSVEP also generally decreases in absolute power as stimulation frequency increases. Importantly, however, the signal-to-noise generally increases with increasing stimulation frequency, likely because power at frequencies above 15 Hz tends to decrease.

The SSVEP approach is an extremely powerful tool when the experimental question requires presenting more than one stimulus on the screen at the same time. Multiple stimuli can be problematic with the ERP approach because the measured response will represent the combination of the responses to all stimuli. While there are a number of approaches that can be used to separate these responses (e.g., computing difference waves, Kutas and Hillyard, 1980) or to configure the stimuli to minimize the contribution of some stimuli (e.g., Hickey et al., 2009), the SSVEP approach can be used to effectively tag specific stimuli with a unique response. One particularly effective use of the SSVEP was reported by Müller et al. (2003). A core question in the spatial attention literature was whether the focus of attention was unitary or whether it could be split into more than one location. To address this question, Müller et al. presented participants with four simultaneous streams of stimuli, two on the left side of the screen, two on the right. Each sequence included a background stimulus that flickered at a different frequency. In different blocks of trials, participants were asked to attend to one stream, two adjacent streams, or two non-adjacent streams. Overall, when attending to a single stream, the amplitude of the SSVEP was larger than when that stream was unattended. A similar pattern was observed when attending to two adjacent streams. In the, split attention condition, the amplitude of the SSVEP at both attended locations was also higher than when those streams were not attended. Importantly, in the split attention condition, the SSVEP response at the intermediate location was no different than in the unattended condition, ruling out the possibility that participants were simply spreading a unitary focus of attention over all three locations. Due to its unique properties, the SSVEP approach has been used to address a range of questions that require the presentation of multiple simultaneous and/or overlapping stimuli (e.g., Andersen et al., 2013; Bullock et al., 2017; Garcia et al., 2013; Meghdadi et al., 2021).

Recent advances and frontiers

In the past 20 years there have been significant advances in computer and electronic design. These advances have made high performance computing easily accessible and they have also dramatically decreased the footprint of EEG recording devices. The combined effect has resulted in the rapid application of machine learning methods to EEG data and the development of protocols for acquiring EEG data on the move.

Machine learning approaches to EEG analysis

The multivariate nature of EEG data has long been recognized (Donchin, 1966), yet for decades, most common analytical approaches have been univariate in nature, involving the aggregation of observed activity across multiple electrodes and trials. While univariate approaches offer computational simplicity and interpretability, they do not completely capture the spatiotemporal dynamics of the EEG signal. Multivariate approaches, on the other hand, while often computationally more intensive, take advantage of the spatiotemporal dynamics of the EEG signal to characterize patterns of brain activity more completely. There has been a dramatic increase in the application of pattern classification and machine learning methods to EEG data, with the number of publications that list machine learning or pattern classification as key words now outpacing those that list event-related potentials as a keyword (**Fig. 2**B). In the late 1990s and early 2000s, the focus of the EEG machine learning literature was on the development of brain computer interfaces. More recently, these approaches have become an essential tool in the cognitive neuroscience literature. There are a variety of machine learning approaches that are used to analyze EEG data, but they predominantly come in two flavors: decoding and encoding models.

Decoding

Decoding analyses aim to discriminate between patterns of neural activity from different categories (e.g., stimuli, behavioral responses, mental states). Models are trained to weight the input features (i.e., measurements of neural activity) that best discriminate between the categories and then are tested on an independent set of data. When performed on EEG data, the typical approach is to train and test using amplitudes (or power) across some set of electrodes at a specific time point as the input features. As a result, the models are capturing the pattern of spatial information that best discriminates between the classes at specific time points. The performance of these models can be quantified in terms of their classification accuracy, sensitivity, specificity, and stability. In cognitive neuroscience, performance is usually compared to chance to determine if there is any meaningful information in the data that discriminates between the classes. Different experimental conditions are also compared to determine if there are changes in the amount of information carried about the categories by the neural activity.

The most widely used class of decoding models are those that assume patterns across the input features in the different categories are linearly separable from one another. Importantly, the models do not make assumptions about the underlying characteristics of the patterns across input features (e.g., spatial distribution), instead they rely on the statistical structure of the data to determine the way the features should be weighted to best discriminate the classes. A classic implementation is a linear discriminant analysis (LDA), which performs dimensionality reduction and enhances class separability by maximizing an objective function (Duda and Stork, 2000). Neither LDA nor any of the other commonly used decoding models were constructed for measurements of neural activity, but rather they are a more general class of machine learning approach that can be applied to a variety of data types. Donchin (1969) first reported that applying stepwise discriminant analysis to single trial evoked responses was feasible. Farwell and Donchin (1988) were one of the first to apply a discriminant analysis to EEG data when they developed a P300-based spelling task, which had the promise of being used as a communication device for patients with little or no motor control. More recently, applying LDA to EEG data has been successful for predicting both individual variations in perceptual categorization and target detection during rapid serial visual presentation (RSVP). When modeling patterns of activity recorded during a perceptual categorization task, LDA has been successful in predicting individual variations in discrimination performance (Das et al., 2010) and has revealed the presence of a neural discrimination component that was not observed with conventional ERP techniques (Philiastides and Sajda, 2006). Parra et al. (2005) were also able to use LDA to capture when targets were detected during a RSVP sequence.

Support vector machines (SVMs) are another popular linear decoder (SVM also has nonlinear variants), which construct a set of hyperplanes that maximally separates the margin between two classes (Das et al., 2010; Parra et al., 2005). Bae and Luck (2018) employed linear SVMs to decode the orientation of a stimulus held in visual working memory (VWM). Models were trained on either the scalp distribution of sustained ERP responses or alpha band activity. While alpha band activity could be used to decode the location of the stimuli, only the models trained on the ERP responses yielded above chance classification accuracy when orientation varied independently of location. This indicates that alpha-band activity only contains location information for memorized stimuli, while ERPs carry information about the feature representation held in WM. Linear classifiers have also been successful in decoding imagined motor movements, emotional states, sleep stages, and the occurrence of epileptic seizures (Abiri et al., 2019; Saeidi et al., 2021).

Encoding

Encoding models aim to characterize not merely whether patterns are different, but rather whether the patterns of neural activity conform to an expected pattern. These models rely on knowledge about experimental design and a priori assumptions regarding the shape of the stimulus (or task) representation space. This information is numerically transformed into a set of basis features in a forward model. Then, the quantitative mapping between the observed input features (e.g., neural measurements) and the forward model is estimated. The resulting estimates can be used to quantify the extent to which the stimulus (or task) space is represented in patterns of neural activity. As a result, encoding models are a powerful tool to test and compare theories about the neural computations that underly cognitive processes (Kriegeskorte and Douglas, 2019; Soto and Ashby, in press).

Forward encoding models applied to EEG data have been used to map the response profiles evoked by naturalistic sounds (e.g., Desai et al., 2021; Di Liberto et al., 2015; Jessen et al., 2019). Typically, auditory stimuli are first decomposed into spectrograms, which are then fed into a forward model to generate multivariate temporal response functions (mTRFs) (e.g., Di Liberto et al., 2015). These mTRFs are feature representations that characterize the properties of an acoustic stimulus that elicit a modulation in the patterns of neural activity. For example, mTRFs can map individual phonemes to larger scale phonetic structures of speech (Di Liberto et al., 2015). Forward encoding models can also be used to characterize temporal response functions that generalize across both tightly controlled speech conditions and more naturalistic speech conditions with multiple overlapping speakers (Desai et al., 2021).

Encoding models have also become a powerful tool for studying visual processing by training a forward model and then inverting the estimated statistical mapping to generate predictions for an independent set of data. The basic steps of this inverted encoding model (IEM) approach are shown in **Fig. 4**. The IEM approach was first applied to EEG data by Garcia et al. (2013). Participants performed a task very similar to that shown in **Fig. 3** that was intended to evoke a SSVEP. The IEM used the spatial distribution of SSVEP power to characterize the extent to which the EEG data carried information about the orientation of the stimuli presented to the participants. Not only were they able to demonstrate that the SSVEP contained information about stimulus orientation, but they also showed that the amplitude of this feature selective response was sensitive to manipulations of attention and modulations in performance. Much like decoding methods, encoding models (both forward and inverted) are relatively agnostic with respect to the input features. All that is needed is some a priori formulation of the nature of the neural responses across the stimulus space. So, not only can the IEM approach be used to track feature selective information, but several studies have applied IEMs to patterns of alpha-band activity map the distribution of spatial attention and track the maintenance of VWM representations (Ester et al., 2018; Foster et al., 2016, 2017; MacLean et al., 2019; Samaha et al., 2016; Sutterer et al., 2019, 2021).

The next frontier of application of machine learning methods to EEG data is the use of deep neural networks. While computationally intensive, deep learning methods have the promise of enhancing discriminative feature extraction at multiple dimensions. The first applications of convolutional neural networks (CNNs) to EEG data were focused on advancing the development of brain-computer interfaces over a decade ago (Cecotti and Gräser, 2008; Cecotti and Gräser, 2011), but there are more recent attempts to use these methods to inform theory (e.g., Vahid et al., 2020).

Machine learning methods, like any method, have shortcomings that must be recognized. For example, machine learning methods are very sensitive to the amount and quality of the training data. In general, more difficult classification problems require more training data of higher quality. Several of the linear methods make specific assumptions about the distribution of the data (e.g., multivariate normal). There are nonparametric approaches, like ensemble classifiers (Cheema et al., 2018) and clustering algorithms that can be combined with feature decomposition methods to avoid this shortcoming (Behri et al., 2018). Encoding models (forward and inverted) have also been criticized on how they are trained and on the grounds that their models are arbitrary (Gardner and Liu, 2019; Liu et al., 2018), but when trained appropriately and used with sensible models constrained by assumptions grounded in the literature, they can be extremely powerful tools or understanding cognition

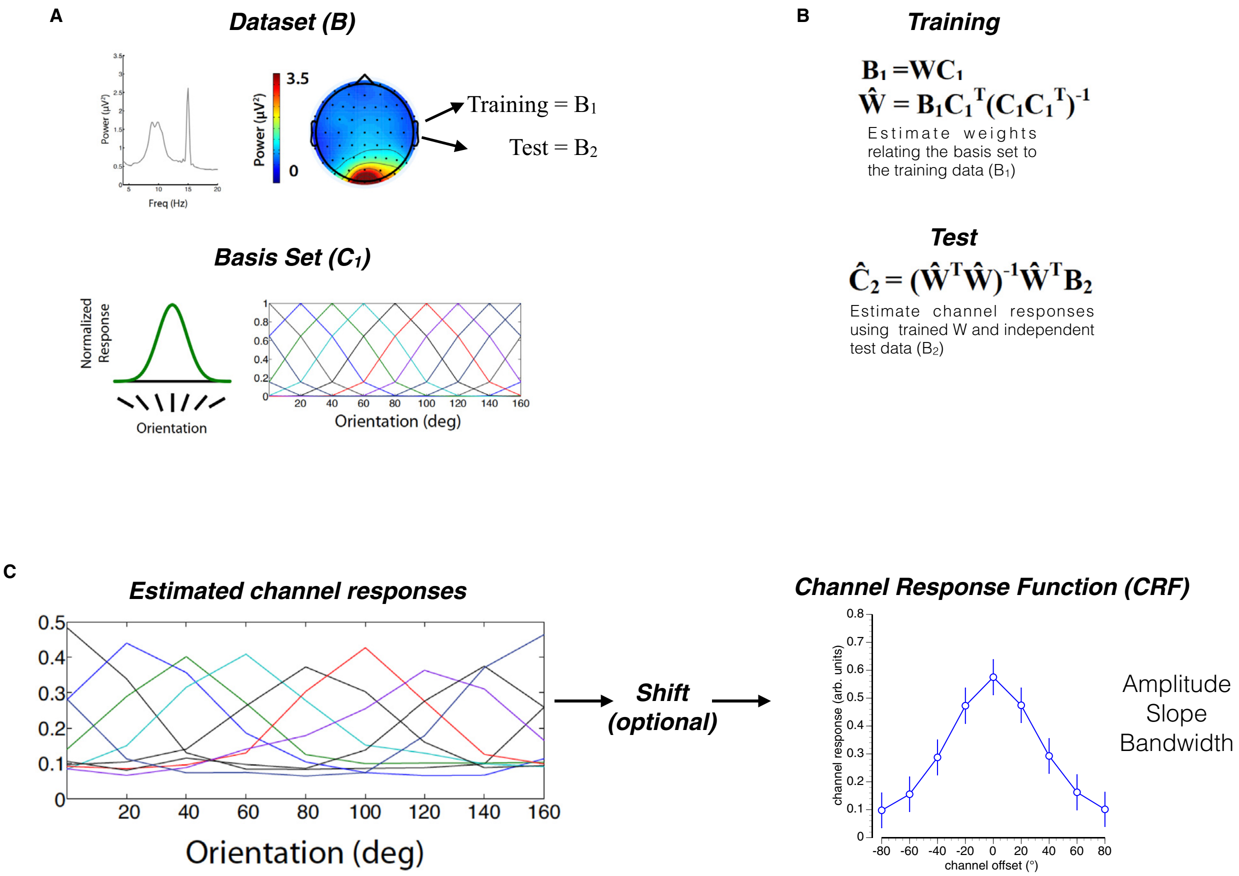

Fig. 4 Schematic of the inverted encoding model approach. (A) Sample SSVEP task dataset (also shown in **Fig. 2**) is separated into a set of training trials (B_1) and a set of test trials (B_2). In each case, each trial contains SSVEP power at each electrode. A model of the predicted response to each of the stimuli across the stimulus space is created. In this example, the basis set (C_1) assumes a peak response at the stimulus location, with the response falling off in a graded fashion. (B) During training, the mapping between the basis set and the data is estimated using an implementation of the general linear model. During testing, the resulting weight (W) matrix estimated during training is inverted and multiplied with the test data (B_2), resulting in the estimated response at each location "channel" (C_2). This process is repeated until all trials serve in both training and test sets. (C) The resulting channel responses can be averaged and because one is typically not concerned with the response to an individual stimulus dimension, shifted to a common point in the stimulus space. The resulting centered channel response function can be characterized in terms of is amplitude, bandwidth, or slope.

(Sprague et al., 2018, 2019). Machine learning methods, especially deep learning approaches, have also been criticized for their lack of interpretability (e.g., Murdoch et al., 2019).

Mobile EEG

Efforts advancing human cognition using EEG are built on the foundation of tightly controlled lab studies in which participants are seated, sometimes with their head fixed in a chinrest, and where the motor requirements of the task are minimal, typically requiring simple key presses or mouse clicks. These experimental task conditions contrast the settings in which real-world tasks are executed, which often require the engagement of the body. The reliance on the traditional lab approach to EEG studies of cognition not only has a philosophical basis rooted in reductionism and the assumed construct validity of the experimental paradigms, but there have also been two key technical challenges to using EEG to study cognition while the body is engaged in motion: (1) the physical constraints of traditional recording hardware and (2) the wide range of artifacts that are caused by movement (e.g., EMG, unstable electrode contact, cable sway). Advances in recording hardware have addressed some of the technical challenges associated with the physical constraints of the recording equipment and have made recording EEG while participants are engaged in physical activity and cognitive tasks both in the lab and outside the lab possible. There has also been progress addressing the technical challenges associated with the artifacts induced by movement. Four strategies have emerged to address movement related artifacts: (1) Take advantage of movement silent periods, (2) Experimental randomization of task-related signals and movement, (3) Experimental separation of movement noise and task-related signals, and (4) Computational separation of noise and task-signals.

Take advantage of movement silent periods

This approach is similar in many ways to early efforts to acquire EEG data in MRI environments (e.g., Herrmann and Debener, 2008). In MRI scanners, changes in the scanner gradients induce large, and consistent, artifacts in the EEG data. However, when the gradients are not changing, the magnetic field is stable, resulting in a much cleaner EEG signal that is closer to what would be collected in a more traditional setting (with the exception of the ballistocardiogram artifact). Just as in these MRI studies, where the task can be designed to introduce electromagnetically stable periods, in a variety of real-world physical tasks, there are periods during which the body is (or can be) stable. For example, when shooting a free throw in basketball, players can pause for a second or more before the shot motion is initiated. These "movement silent" periods are ideal times when clean EEG data can be acquired and be related to performance on the task. Chuang et al. (2013) acquired EEG from basketball players executing free throws and compared preshot midline frontal theta as a function of whether the shot was subsequently made or missed. Similarly, several studies have also used this approach to relate brain activity to shot precision or expertise when using a rifle (e.g., Doppelmayr et al., 2008; Hillman et al., 2000). The primary advantage of this approach is that the EEG data can be processed with relatively standard techniques and do not require a lot of conditioning. The disadvantage is that the experimental tasks need to incorporate movement silent periods and some real-world tasks may not be amenable to such changes.

Experimental randomization of task-related signals and movement

As summarized in **The event-related potential technique** section, the success of the event-related potential technique rests on the assumptions that electrical sources sum in a linear fashion, sources of noise are random with respect to task-related signals of interest, and task-related signals are consistent across trials. If these assumptions are satisfied, then averaging across trials serves to effectively remove the noise from the averaged signal. To the extent that movement-related noise acts like other sources of noise, then this approach can reasonably be applied to extract event-related responses during movement. For example, Bullock et al. (2015) used an odd-ball task and the ERP technique to identify the stages of information modulated during brief bouts of physical exercise of different intensities relative to rest. Importantly, biking intensity was varied by manipulating pedaling resistance while holding cadence constant (paced with a metronome), thereby roughly equating the motion artifact across conditions. In addtion, the cycling cadence was not synchronized with the task. The analysis of the ERP data revealed a modulation of the visually evoked P1 ERP component as a function of low intensity exercise compared to rest. In addition, the latency of the P3a evoked by rare distractors was faster under low intensity exercise than under rest or high intensity exercise (**Fig. 5**). Scanlon et al. (2020, 2019) have used a similar approach during cycling outside the lab and have shown that auditory evoked responses are modulated by the environmental context. Several studies have adopted the same approach during walking (Bradford et al., 2019; Cao and Händel, 2019; Jacobsen et al., 2021) and a variety of other mobile tasks (for a review see Gramann et al., 2014). Artifacts caused by walking are somewhat more challenging to deal with because of the wide range of variability from step to step, but nevertheless these studies, like the cycling studies, have shown that randomization of task-related signals and movement related artifacts is a powerful tool for measuring brain activity when engaged in locomotive behaviors.

Experimental separation of task-related signals and movement-related noise

Some physical activities, such as cycling and walking, require repetitive motion over sustained periods of time. These repetitive motions induce EEG artifacts that carry power at the frequency of the repetition. One strategy for dealing with artifacts of this type is to design the experimental protocol so as to avoid EEG task-related signals in the same frequency. For example, Bullock et al. (2017), presented participants with oriented gratings that flickered at 15 Hz while they cycled at a cadence of 50 beats per minute. The 15 Hz flicker induced an SSVEP peaking at 15 Hz, which was not only lower than the frequency of the cycling cadence, but lower than frequencies that typically carry EMG activity from sustained muscle contraction. The power of the SSVEP across electrodes was modeled using the IEM approach (see section **Encoding**) to assess the quality of the orientation selective information carried in the EEG signal. The amplitude of the resulting channel response functions were higher at low exercise intensity relative to rest and high exercise intensity, indicating that feature selective activity in the human brain is modulated by locomotive behaviors, a result that bears remarkable similarity to the impact of locomotive behaviors on sensory coding in other species (e.g., Chiappe et al., 2010; Eriksen et al., 2014; Maimon et al., 2010; Neill and Stryker, 2010). This approach can also be applied to oscillations in other frequency bands, so long as they are separate from the frequencies that carry the movement related noise. For example, Garrett et al. (2021) had participants execute a spatial working memory task during exercise and rest. IEM models were then trained and tested using alpha power to reconstruct the remembered location. Alpha power carried robust information about the remembered stimulus location throughout the trial in both conditions, although the quality of the reconstructions was degraded during exercise.

Computational separation of task-related and noise signals

The strategies outlined above attempt to avoid the movement-related artifacts altogether, but another effective strategy has been to estimate or model the noise components and then correct the EEG signal. There are three main types of computational approaches. The first uses independent component analysis (Makeig et al., 1996). For example, Gramann et al. (2010) had participants execute an oddball task while walking on a treadmill and while their EEG was recorded. After using ICA to remove the motion artifacts, these authors observed characteristic visually evoked responses when walking at different speeds that were similar in amplitude and timing to those observed when stationary. The ICA approach rests on the assumption that the movement-related artifacts are consistent and independent sources from the task-related signals. The second computational approach, which can be combined with the

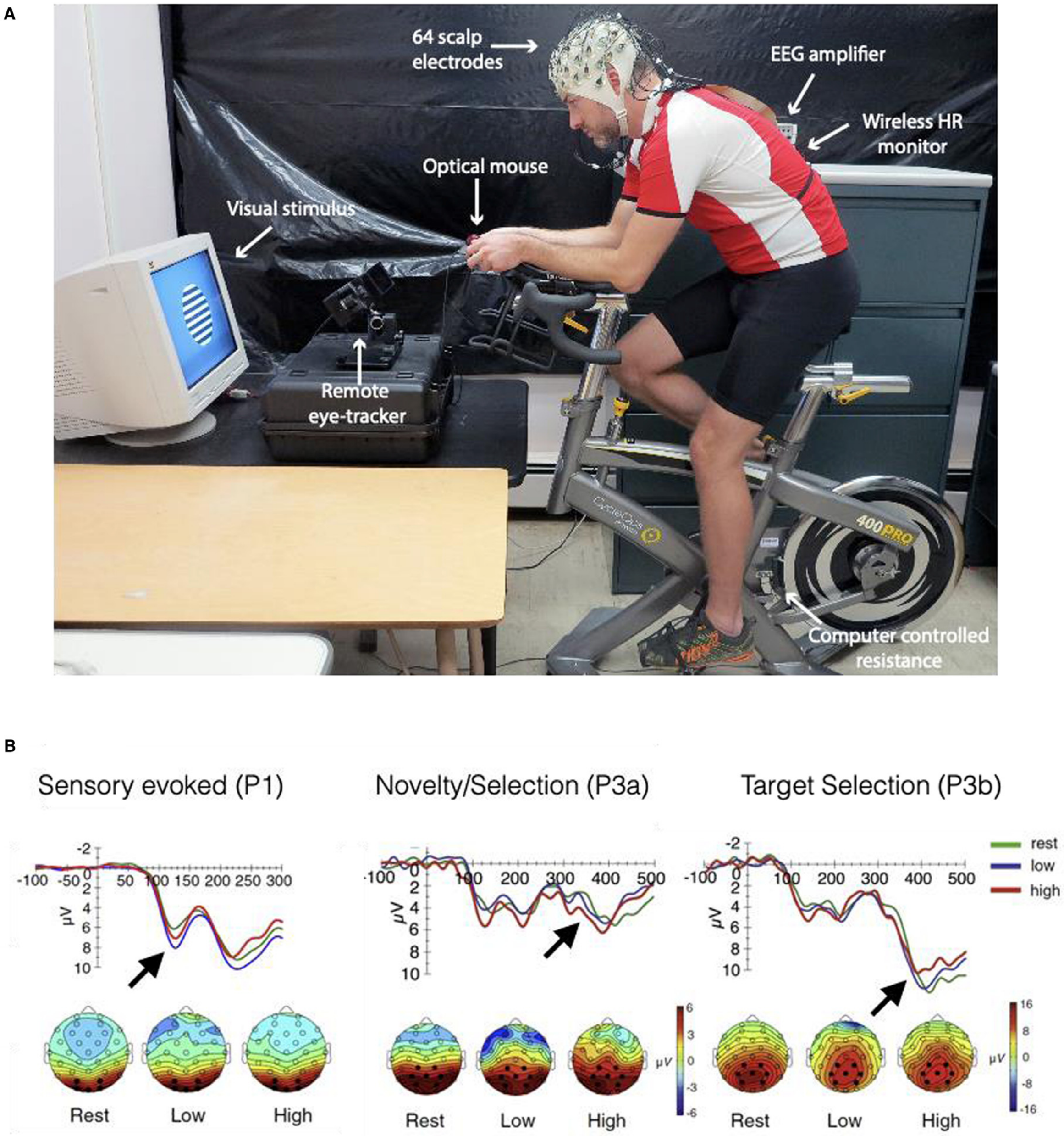

Fig. 5 Example experimental set-up and results from EEG studies in which participants were engaged in physical activity while performing a cognitive task. (A) Example experimental set-up for an EEG study performed while participants ride on a stationary bike. (B) ERP results from an odd-ball task executed while participants were seated still on a stationary bike or rode at low or high intensities. The sensory evoked response to the standard (frequent) stimuli in the task show a visual P1 ERP (measured at occipital electrodes), the amplitude of which was largest at low cycling intensity. The response to the rare distractor stimuli (P3a) at parietal occipital electrodes had a faster onset under high intensity exercise. The response to the rare target evoked a large P3b ERP that was not modulated by exercise. (A) Adapted from Bullock et al. (2017); (B) Adapted from Bullock et al. (2015).

ICA approach or can be used in isolation, is to create models of the noise using electrodes that do not measure brain activity, but rather just artifacts induced by the physical movement of the electrodes or cables (Nordin et al., 2018; Symeonidou et al., 2018). These model signals then can be subtracted from the EEG signal of interest. A related approach is to use EEG head phantoms that can be used to estimate the impact of movement on known (simulated) signals (Oliveira et al., 2016). The third computational approach is to use deep learning frameworks. For example, Ding et al. (2019) used both minimally preprocessed scalp and nonscalp electrodes (EOG and EMG) as inputs to a novel deep learning architecture with a temporal autoencoder at the frontend and EEGNet (Lawhern et al., 2018) at the back end to classify target related responses when participants were performed an oddball task during exercise (Bullock et al., 2015). Even when using minimally processed data this deep learning approach outperformed EEGNet when it was trained and tested on data processed with more typical pipelines.

Conclusion

Electroencephalography is the first neuroimaging technique that allowed scientists and clinicians to have direct, noninvasive access to the internal workings of the brain. This powerful tool has led to many foundational discoveries about the temporal properties and capacity of human cognition. The significant advances in hardware, methodology, and computational approaches over the past 20 years have allowed investigators to push the boundaries of the experimental tasks and contexts within which it is possible to acquire EEG data. While significant challenges remain that would allow for chronic EEG data acquisition, the capacity to acquire EEG data while people are engaged in physical activities and outside the lab has the potential to provide a richer understanding of human cognition and how it supports daily activities from the mundane to the extreme.

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