

EEG-based neurophysiological indices for expert psychomotor performance – a review

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ABSTRACT

A primary objective of current human neuropsychological performance research is to define the physiological correlates of adaptive knowledge utilization, in order to support the enhanced execution of both simple and complex tasks. Within the present article, electroencephalography-based neurophysiological indices characterizing expert psychomotor performance, will be explored. As a means of characterizing fundamental processes underlying efficient psychometric performance, the neural efficiency model will be evaluated in terms of alpha-wave-based selective cortical processes. Cognitive and motor domains will initially be explored independently, which will act to encapsulate the task-related neuronal adaptive requirements for enhanced psychomotor performance associating with the neural efficiency model. Moderating variables impacting the practical application of such neuropsychological model, will also be investigated. As a result, the aim of this review is to provide insight into detectable task-related modulation involved in developed neurocognitive strategies which support heightened psychomotor performance, for the implementation within practical settings requiring a high degree of expert performance (such as sports or military operational settings).

1. Introduction

A primary objective of human neuropsychological performance research is to define the physiological correlates of adaptive knowledge utilization (i.e., the creative and/or flexible application of knowledge under various parameters), and thus, to characterize fundamental processes underlying efficient psychometric performance (A. C. Neubauer et al., 2004). Such goals enable humans to operate more efficiently, both at repetitive and complex tasks, with overall decreased conscious effort. In context, psychomotor performance refers to the capacity, flexibly, and speed of the nervous system, defined by metrics such as vigilance, accuracy, coordination, and attention (Hindmarch, 2014). Interestingly, both cognitive and motor processing stem from homologous evolutionary derivatives (Mendoza & Merchant, 2014), and are therefore controlled by similar anatomical corticostriatal loops (i.e., in the basal ganglia; Middleton & Strick, 2000). In addition to the basal ganglia, brain regions such as the frontal lobe and cerebellum govern executive functions which also relate to both cognitive and motor processes (Lotan et al., 2016). This indicates that forms of cognitive processing (such as attention, perception, and memory – all of which form the basis of intelligence; Colom et al., 2010), coalesce with motor-based processing

(such as sensorimotor processing, visuospatial cognition, motor planning, etc.), in order to support the execution of psychomotor performance (Lotan et al., 2016). As psychomotor performance encapsulates the effective integration of both cognitive and motor neural pathways, the bidirectional influence involved in both forms of processing (Lotan et al., 2016), allows for a dynamic neurophysiological model defining psychomotor performance to be made. For this reason, the enrichment of the current neurophysiological models encapsulating heightened performance, is not only critical to the execution of everyday tasks, but especially holds importance for the performance of tasks within specialized domains. Such models, therefore, are proposed to support the enhancement of both skill acquisition and execution, across various domains of expertise.

Skill execution, referring to the ability to complete a specific task and/or goal, has historically been classified into the three predominant divisions: beginner (i.e., novice), intermediate, and advanced (i.e., expert; Fitts, 1967), where experts can be said to be more effective, efficient, and require less effort overall when performing tasks for which experts are familiar, compared to those who are learning a skillset. For instance, higher cognitive abilities have been negatively correlated with metabolic rates (i.e., cerebral glucose metabolism; Haier et al., 1988),

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and intelligence has been found to correlate with overall more efficient brain functioning (i.e., requiring less neuronal resources in order to execute a task; Haier, Siegel, Tang, et al., 1992). The beginners' process involves intentional and effortful analysis, meaning that novice psychomotor performance may be characterized by an amplified mental and verbalization processing and effort (Haufler et al., 2000). Such amplification of perceived effort, therefore, can be thought to act as a means to facilitate strategies of self-instructions during skill acquisition (i.e., the development or improvement of a skill) in order to support task execution (Abernethy & Russell, 1987; Dorothy V. Harris & Bette L. Harris, 1984; Robert N. Singer et al., 1993).

Where intermediate performance may comprise task execution involving degrees of concentration, expert task-execution may be quantified as being superior to novice and intermediate performance, deriving from a skillset which has become progressively more established with practice. Further, the experience of cognitive ease within the execution of specialized skillset, and exhibition of relative automation are characteristic of expert performance (Fitts, 1967; Holyoak, 1991). In addition, highly skilled motor-based performers can be characterised by a superior ability to extract and process salient environmental cues, which pre-empts and instigates suitable psychomotor responses (Landers, 1991). For this reason, the minimized energy expenditure associated with high degrees of performance is posed to exist in form of the 'neural efficiency' hypothesis (Del Percio et al., 2009; A. C. Neubauer & Fink, 2009). The 'neural efficiency' hypothesis concerns how more 'capable' individuals show less neuronal activation in order to perform a task than less capable or intelligent individuals, particularly outlined for tasks of moderate difficulty (Dunst et al., 2014).

Within the present article, electroencephalography-based neurophysiological indices encapsulating expert psychomotor performance, will be explored. As a means of characterizing fundamental processes underlying efficient psychometric performance, the neural efficiency model will be evaluated in terms of alpha-wave-based selective cortical processes. Cognitive and motor domains will initially be explored independently, which will act to encapsulate the task-related neuronal adaptive requirements for enhanced psychomotor performance associating with the neural efficiency model. Moderating variables impacting the practical application of such neuropsychological model, will also be investigated. As a result, this review aims to provide insight on detectable task-related modulation involved in developed neurocognitive strategies which support heightened psychomotor performance, for the implementation within practical settings (such as sports or military operational settings).

2. Methods

The present article was constructed using a literature search spanning over the past 60 years (1963– Q2 2023) through databases including PubMed, ScienceDirect, and Google Scholar. Key words were searched both alone and in combination, which included: electroencephalogram (EEG), psychomotor, cognitive, motor, neurocognitive, performance, neural efficiency, and alpha-waves. Bibliographies of yielded articles were cross-checked with the database results, to ensure that no significant articles and/or alternative search terms were omitted. Studies of higher relevance, higher methodological quality, and of a more recent published date were selected in this narrative review, when more than one study were available. Conference presentations, single-subject case studies, and anecdotal reports were excluded from this review.

The yielded motor-based research included studies using sports such as: karate, fencing, football, cycling as a means of investigation, whereas studies of exploratory focus within the motor-based visuospatial domain used sports such as archery, shooting, and golf. Due to an identified trend of focus within the "neural efficiency" literature on intelligence and memory, this review predominantly used such modalities on as the basis of discussion for the cognitive segment of the review. As the

primary focus of this review was EEG-based neuronal markers of expert psychomotor performance, publications solely employing alternative neuroimaging (such as fMRI), were not prioritized.

3. The quantification of neural indices for spatially selective cortical processes

Various neuroimaging techniques have been used in order to investigate the neural correspondences of both cognitive and psychomotor performance, such as: positron emission tomography (PET), single photon emission computed tomography (SPECT), functional magnetic resonance imaging (fMRI), and electroencephalogram (EEG) (Charlot et al., 1992; Haier et al., 1988, 2004; Haier, Siegel, MacLachlan, et al., 1992; Parks et al., 1988; Ruff et al., 2003; Rypma et al., 2002, 2005; Rypma & D'Esposito, 1999). The EEG, being of the oldest neuroimaging techniques, measures the electrical oscillatory properties of the brain which are determined by intrinsic dynamics of neuronal membrane and synaptic processes, the strength of network interconnection, and local or global neurotransmitter modulatory influence (Lopes da Silva, 1991; Singer, 1993). With selective information processing being reliant on neural oscillations in the brain (Erol Başar, 1999; Fries, 2005; Pfurtscheller & Lopes da Silva, 1999; Varela et al., 2001), the subsequent subdivided of cortical neural oscillations are segmented into the following frequency bands: delta (δ), theta (θ), alpha (α), beta (β), and gamma (γ) (Niedermeyer & Lopes da Silva, 1982).

Interconnections between neuronal networks are often formed by feedback loops which exist at varied distances (Lopes da Silva, 1991; Singer, 1993). Of most relevance, thalamo-cortical and cortico-cortical loops exist through functional oscillatory modes, which both facilitate and inhibit the transmission of sensorimotor and cognitive information within the brain (Brunia, 1999; Deeny et al., 2003; Pfurtscheller & Lopes da Silva, 1999; Steriade & Llinás, 1988). Furthermore, the physiological mechanisms involved in such loops are reflected in alpha and beta oscillations in the brain (Lopes da Silva, 1991), where beta oscillations are associated with motor-based observations, planning, and preparations (Brinkman et al., 2014; Denis et al., 2017), and alpha rhythms are related to sensorimotor processing, visuospatial attention, cognitive and memory performance, action observation, and movement planning (Klimesch, 1997, 1999, 2012; Klimesch et al., 2007, 2011; Minarik et al., 2018; Quandt et al., 2011; ter Horst et al., 2013; see Table 1, which provides a fundamental outline of EEG-based frequency band spectrums and their corresponding characteristics). Interestingly, alpha rhythms, sometimes referred to as Berger rhythms, are also directly associated to a degree of wakefulness and attention (Klimesch, 1999), as well as skill development (Smith et al., 1999). For this reason, the alpha band will predominantly form the basis of the discussion to characterize psychomotor performance, particularly for the role it plays in both global attentional and task-specific processes (Klimesch, 1996; Klimesch, Doppelmayr, et al., 1998; Klimesch, 1999), although other frequency bands, such as the theta and beta bands, will also be mentioned where context is relevant.

Within the interconnectivity of alpha band power in psychomotor performance, a critical distinction between tonic and phasic changes in powers requires noting (Klimesch, 1999). Foremost, tonic changes in powers are associate with slower neurophysiological responses which are neither readily nor intentionally modified (Klimesch, 1999). The neurophysiological variables which impact tonic changes in power are those which accumulate over the course of months or throughout a lifetime (Huang et al., 2008, 2009), due to how tonic changes are often consequential of non-volitional neurophysiological processes (such as circadian rhythms, neurological disorders, fatigue, etc.; Lin et al., 2010; Santamaria & Chiappa, 1987). Resultantly, tonic changes may be measured during 'resting' states, i.e., while no task is being executed, which are used as baseline or reference measurements for subsequent task-related investigations – known as phasic changes.

Phasic changes are thought to occur readily, such as in response to a

Table 1
A simplified outline of EEG-based oscillatory band spectrum (adapted from: Schomer & Lopes da Silva, 2010).

Frequency Band (Hz)	Primary behavioral characteristics associated with each frequency band	Main forms of research investigations that characterize each frequency band
delta (δ ; 1–4), theta (θ ; 4–8),	<ul style="list-style-type: none">• Deep non-REM sleep (i.e., slow-wave sleep)• Encompasses cognitive processes underlying working memory• Alters with changes in consciousness and drowsiness• Acts as a long-distance carrier of brain oscillations across cortical regions	<ul style="list-style-type: none">• Sleep• Sleep disorders• Mental workload• Meditation• Propensity to sleep
alpha (α ; 8–13),	<ul style="list-style-type: none">• Suppresses with the opening of the eyes• Changes in response with stimuli/events	<ul style="list-style-type: none">• Wakefulness and attention• Visuospatial processing• Visuospatial processing• Sensorimotor processing• Cognitive and memory performance• Action observation• Movement planning• Biofeedback training• Stimulus-induced alertness• Motor control and motor-based observations, planning, and preparations
beta (β ; 13–30),	<ul style="list-style-type: none">• Active concentration/intensive thinking• Activity alters in accordance with motor planning and execution	<ul style="list-style-type: none">• Motor control and motor-based observations, planning, and preparations
gamma (γ ; 30–100)	<ul style="list-style-type: none">• Facilitates the binding sensory impressions of objects to coherent form• Involved in neural processes, such as eye movements and micro-saccades	<ul style="list-style-type: none">• Micro-saccades

task or present stimuli. For this reason, phasic changes are quantified in respect to reference changes (i.e., tonic; Doppelmayr et al., 2002), and provide insight on the alpha-related modulation endured due to an event and/or visuo-motor task performance (Del Percio et al., 2009). Although tonic changes in power amplitudes are highly associated with cognitive performance changes (Doppelmayr et al., 2002), phasic changes in alpha power, also known as event-related changes, may be used as an index for spatially selective cortical activation (Klimesch, Doppelmayr, et al., 1998; Klimesch, Russegger, et al., 1998; Pfurtscheller & Aranibar, 1977). For this reason, event related changes may be quantified as the percentage of band power lost during a task, in respect to rest/reference interval as a means of quantifying spatially selective cortical activation (Pfurtscheller & Aranibar, 1977; Pfurtscheller & Lopes da Silva, 1999). Subsequently, controlled on a local basis, neuronal and intraneuronal interactions are reflected in measurable increases or decreases in relative power amplitudes frequency components of EEG signals (Pfurtscheller & Lopes da Silva, 1999). With measurable increases in power amplitudes compared to baseline/reference values known as Event-Related Synchronization (ERS; Pfurtscheller, 1992), relative decreases in power amplitudes are referred to as Event-Related Desynchronization (ERD; Pfurtscheller, 1977; Pfurtscheller & Aranibar, 1977; Pfurtscheller & Lopes da Silva, 1999). As the increase in cell assembly, and thus, the involvement of neural networks (i.e., cooperation between large number of neurons deriving from a summation of synaptic events; Pfurtscheller et al., 1996; Pfurtscheller & Lopes da Silva, 1999), results in a reduction in synchrony of oscillation across detected neuronal populations, a suppression in relative powers (ERD) during cognitive processing implies a reduction in synchrony of oscillation across detected neuronal populations (Pfurtscheller & Lopes da Silva, 1999). This means that within the alpha band, ERD indicates greater cortical activity relative to baseline (Lindsley & Wicke, 1974), whereas enhanced synchrony (ERS) between neuronal populations indicates a decrease in cortical recruitment (see Fig. 1; Lindsley & Wicke,

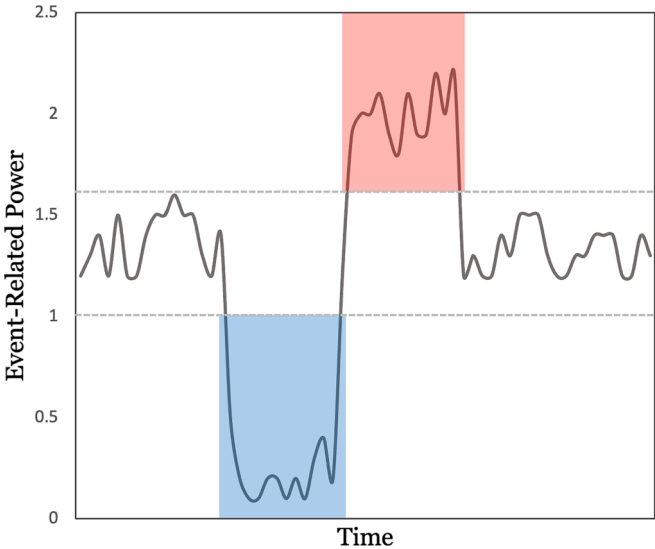


Fig. 1. A schematic representation of electroencephalography-based event-related changes in power with time. The baseline power range is depicted as the activity within the dotted line. Increases in relative powers from baseline conditions are represented in red, which represent event-related synchronization (ERS). Relative decreases in power amplitudes depict event-related desynchronization (ERD) and are represented in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1974). Although alpha band ERSs were initially thought to reflect reduced state of active information processing in the underlying neuronal networks (Pfurtscheller et al., 1996), and thus cerebral inactivity (i.e., cortical ‘idling’; for review see Klimesch et al., 2007; Pfurtscheller & Lopes da Silva, 1999), ERS are now thought to not merely reflect cortical deactivation (e.g., Cooper et al., 2003; Jensen, 2002; Klimesch, Doppelmayr, et al., 1999; Ray & Cole, 1985), but are additionally interpreted as a functional correlate of inhibition or top-down control (Klimesch et al., 2007; Sauseng et al., 2005). For this reason, alpha band ERS (i.e., increased in relative spectral power) represent cortical inhibition, whereas ERDs in relative spectral powers are indicative of cortical excitation (i.e., excitatory processes), or the release of inhibition (Pfurtscheller & Lopes da Silva, 1999).

Furthermore, the inverse relationship alpha power with cortical regional activation partially derives from the observation that most cognitive tasks were accompanied by alpha band desynchronization (ERD) when comparing alpha potentials to a pre-stimulus reference state (Fink & Benedek, 2014). With higher performance execution associating with a decreased requirement of neural resources (Nunez & Williamson, 1996; Smith et al., 1999), this indicates that more efficient neural processing may relate to neural organizations in the form of less prominent cortical activation, and thus less ERD (Doppelmayr, Klimesch, Hödlmoser, et al., 2005), or alpha ERS (Smith et al., 1999). Practice-related increases in alpha powers supports the inverse relationship between ERD detection and performance, which have contributed to the manifestation of the ‘neural efficiency’ hypothesis (Neubauer et al., 1995). Although the negative relationships between ERD and performance have been identified within numerous studies, the reverse has also been identified (i.e., against the ‘neural efficiency’ hypothesis; e.g., Doppelmayr, Klimesch, Hödlmoser, et al., 2005). For this reason, the sections to follow will discuss the veracity of such reorganization of activation as an index for performance, both within cognitive and motor-based performance domains. Factors and mediators impacting the validity of such a model will then be explored as a means of consolidating how the knowledge of such markers may be used within practice.

3.1. Neural correlates associated with varying degrees of cognitive performance

As psychomotor performance integrates both cognitive and motor neural pathways, understanding correlates of cognitive performance, supports the encapsulation of salient neural markers for psychomotor performance. Within neuroimaging studies, correlates of intelligence and memory performance have been tested using indices such as event-related potentials (ERP; Mirand et al., 2019; Van Rooy et al., 2001), and cortical coherence (Jaušovec & Jaušovec, 2001; Park et al., 2021; Thatcher et al., 2005), source locations (Jaušovec & Jaušovec, 2004), alpha power (Doppelmayr et al., 2002; Klimesch, Vogt, et al., 1999), alpha frequency (Anokhin & Vogel, 1996; Clark et al., 2004; Rathee et al., n.d.) and event-related desynchronization/synchronization (ERD/ERS; Doppelmayr et al., 1998; Jaušovec & Jaušovec, 2000; A. Neubauer et al., 1995; A. C. Neubauer et al., 2004; Wianda & Ross, 2019). With neural efficiency depicting more effective organization of cortical functions with increases in performance, ERDs (being interpreted as correlates of cortical activation; Klimesch, 1999) therefore are used as a measurable method of neural effort (Pfurtscheller & Lopes da Silva, 1999). For this reason, as a manifestation of cortical neural efficiency, ERD quantification has been used to parameterize a notably significant relationship between memory (Klimesch et al., 1997) and intelligence (Doppelmayr, Klimesch, Sauseng, et al., 2005; Grabner et al., 2003, 2004; Jaušovec & Jaušovec, 2000, 2003, 2004; Klimesch et al., 1997; A. Neubauer et al., 1995; A. C. Neubauer et al., 2004, 2005; A. C. Neubauer & Fink, 2003; Stipacek et al., 2003). For instance, within a review investigating 54 neuroimaging studies (such as fMRI, PET, EEG, etc.) involving a variety of cognitive tasks, it was found that majority of the studies ($k = 29$) concurred with the idea of neural efficiency, with 16 studies producing mixed evidence and (i.e. depend upon moderator variables), and 9 finding positive correlations between intelligence and brain activation (See review: Neubauer & Fink, 2009).

More specifically, alpha ERD has been shown to be less prominent in those with higher intelligent quotient (IQ) during cognitive and working memory tasks (Grabner et al., 2004, 2006; A. Neubauer et al., 1995; A. C. Neubauer et al., 1999, 2004; A. C. Neubauer & Fink, 2003), with widespread ERD being associated with memory and perceptual/judgment tasks (Grabner et al., 2007; Klimesch et al., 1994; Peng et al., 2015; Pfurtscheller & Klimesch, 1992; Serman et al., 1996). Although high ERD has also been associated with high cognitive performance (Jaušovec & Jaušovec, 2004; Klimesch et al., 1997), overall higher intelligence and cognitive performance has been shown to be associated with smaller alpha ERD in a variety of different tasks (Grabner et al., 2003, 2004; A. Neubauer et al., 1995; A. C. Neubauer et al., 1999, 2004, 2005; A. C. Neubauer & Fink, 2003).

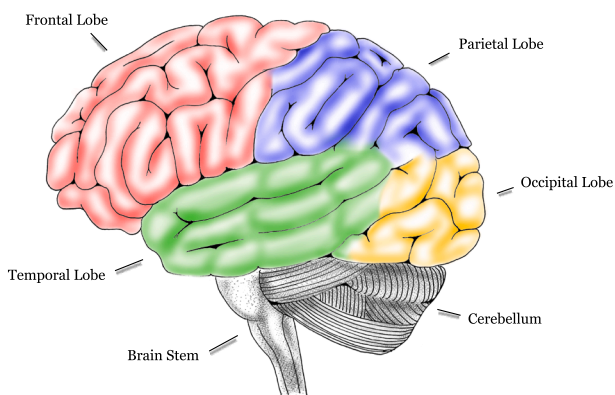


Fig. 2. A schematic of the human brain depicting the four primary lobes: frontal, parietal, temporal, and occipital. Figure produced by Jazmin M. Morrone.

With human intelligence being most prominently associated with frontal and parietal regions (see Fig. 2 for contextual support; see review: Jung & Haier, 2007), the efficiency of cognitive processing, also known as fluid intelligence, has been supported by the fronto-parietal integration theory (i.e., the largescale connection of such brain regions being the underlying biological basis of intelligence; e.g., Colom et al., 2009; for a review see: Deary et al., 2010). In alignment, neuroimaging studies probing regional detection of activity during cognitive processing have shown weaker fronto-parietal activation to be associated with higher intelligence markers (such as IQ, working memory, word fluency, and spatial skills; Charlot et al., 1992; Haier et al., 1988, 2004; Haier, Siegel, MacLachlan, et al., 1992; Parks et al., 1988; Ruff et al., 2003; Rypma et al., 2002, 2005; Rypma & D'Esposito, 1999). As fluid intelligence has been said to depend on the integrity of white matter connections between the regions (Barbey et al., 2014; Jung & Haier, 2007), using cortical selectivity within such regions, therefore has resulted in a large support of neural efficiency (i.e., weaker activation). Although some have shown stronger fronto-parietal activation with cognitive performance (Gray et al., 2003; Newman et al., 2003), overall weaker fronto-parietal activation has presented as a salient marker of cognitive performance, such as intelligence. For this reason, weaker alpha activity localized within fronto-parietal regions may be said to account for neural efficiency within cognitive task domains. Although, mediating factors impacting such index of selective cortical processing (see following sections), must be considered.

3.2. Neural basis for high degrees of performance in motor-based domains

Reiterated, physiological explanations of psychometric performance indicate that less neural resources are required by those performing a high degree of expertise. As a result, ideal athletic performance may be characterized as focussed and effortless task execution, whereby both global and locally lower cortical activity act as an index for spatially selective cortical processes (i.e., neural efficiency; see Fig. 3 for a schematic outline; Del Percio et al., 2009). Interestingly, a meta-analysis found athletes to have overall better cognitive performance compared to non-athletes, whereby expert athletes exhibited less brain activation (thus less ERD, or greater ERS) during both resting state and task performance (both cognitive and motor), compared to non-athletes (Voss et al., 2010). As an example, elite athletes within the domain of karate have exhibited less cortical activation over frontal, central, parietal and occipital site locations in awake resting states (Babiloni et al., 2010; Del Percio et al., 2011), during conditions of standing eyes-closed upright (Del Percio et al., 2010), while performing simple voluntary hand movements (Del Percio et al., 2010), and during a mental arithmetic task (Duru & Assem, 2018), compared to non-athletes.

Neural efficiency has also been exhibited by elite cyclists during cycling compared to control groups, as defined by decreased alpha ratios associating with high maximal aerobic power (Ludyga et al., 2016), as well as within professional dancers, as defined by stronger posterior parietal ERS compared to novices (Fink et al., 2009). In addition, karate athletes have been found exhibit less pronounced alpha ERD in dorsal and frontoparietal cortical regions (so called “mirror” pathways) when observing performances and actions, compared to non-athletes (Babiloni, Marzano, Infarinato, et al., 2010). As this observation-based reactivity was additionally demonstrated in gymnasts when viewing media from real performances (i.e., competitions; Babiloni et al., 2009), these findings indicate that expert athletes demonstrate ‘neural efficiency’ relating with social cognition (Babiloni, Marzano, Infarinato, et al., 2010), inferring that neural efficiency is not only prominent during task execution, but also during motor imagery responses. In support of this, expert tennis table players displayed decreased frontoparietal alpha ERD during motor response imagery via simulation serves compared to novices (Wolf et al., 2013), substantiating the manner in which neural efficiency may play in a wide range of motor-based domains.

Decreases in cortical activity (i.e., enhanced alpha rhythm power

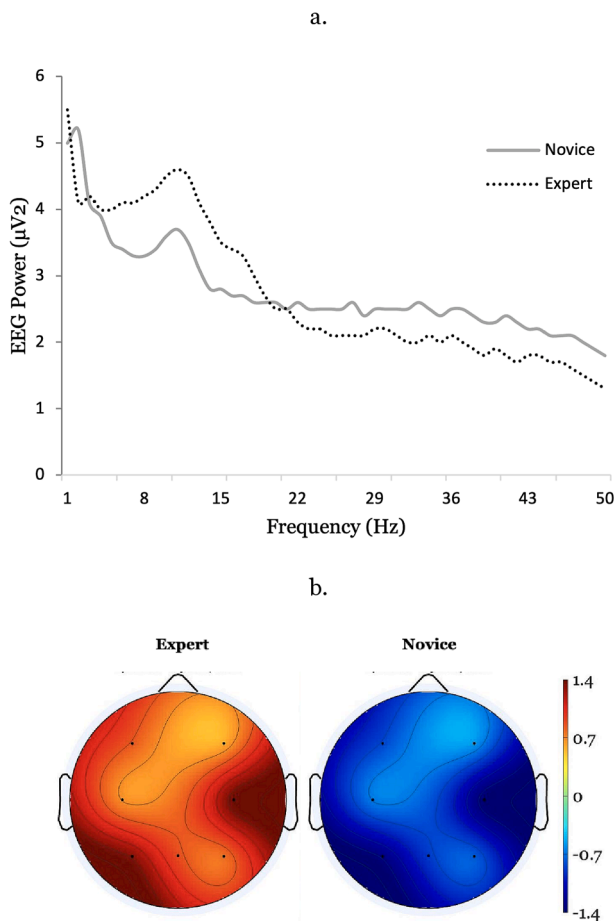


Fig. 3. (a) A schematic representation of relative global event-related power (μV^2) comparisons of novice and expert neural activity. As postulated by the neural efficiency hypothesis, the experts are posited to display decreased cortical activation (i.e., increased relative powers) during tasks, compared to novices within the alpha frequency range (8–12 Hz). (b) A schematic representation of statistical topographical plots displaying normalized parametric differences of the interindividual differences in Power Spectrum Densities ($\mu V^2/Hz$) between experts and novices within the alpha range (8–12 Hz). Positive values (red) indicate relative increases in powers (i.e., event-related synchronizations; ERS) in comparing groups, and relative decreases in power (blue) represent relative event-related desynchronizations (ERD). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ERS or less ERD), have also been associated with higher degrees of accuracy in golf putting (Babiloni et al., 2008; Crews & Landers, 1993; Gallicchio et al., 2017) and pistol shooting (Kerick et al., 2004; Loze et al., 2001). More specifically, during shooting preparation (i.e., 6 s duration pre-shot), lower alpha ERD has been found in expert shooters over controls in occipital areas (Haufler et al., 2000; Janelle et al., 2000; Loze et al., 2001), parietal (Baumeister et al., 2008) and the whole scalp (Del Percio et al., 2009). Interestingly, ERD was also found to increase after worst shots in expert pistol shooters (Loze et al., 2001). During aiming period of target shooting tasks, experts show increased left central, temporal, and parietal regions alpha (10–11 Hz) power, as well as global increases in theta, beta, and gamma power (Haufler et al., 2000; J. Zhang et al., 2021). These findings were attributed to suppressions in visual attention, and thus, exhibiting less cortical effort to process necessary information to perform the task (Loze et al., 2001). For this reason, decreased brain activation has been said to associate with greater accuracy within targeting sports, such as within pistol shooting (Loze et al., 2001) and elite marksmen (Janelle et al., 2000; J. Zhang et al., 2021).

Source localized evidence of selective neural activity within aiming professions (i.e., target sports, such as shooting) shows higher left lateralized alpha power during the final seconds before shots compared to novices, which was predominantly found over anterior-temporal cortex (Haufler et al., 2000; Janelle et al., 2000; Kerick et al., 2004; Landers et al., 1994; Loze et al., 2001). Although a significant increase in left hemispheric (LH) alpha power was identified within elite marksmen (i.e., ERS; Janelle et al., 2000; Zhang et al., 2021), the same pattern of localized activity was found to associate with worse precision in elite marksmen (Salazar et al., 1990). Interestingly it has been shown that the act of practicing a skillset coincides with the portraying of dominant LH alpha ERS (while displaying constant right hemispheric activity), as elicited by novice participant practicing the task of archery (Kerick et al., 2004; Landers et al., 1994). Furthermore, LH dominant alpha ERS (particularly, left anterior temporal regions) are also found to associate with lower degrees of visual-based target analysis (Loze et al., 2001). With greater LH inhibitory power increase inferring quieting within the left hemisphere, the economy of cortical processing reflected in reactivity of alpha power in elite precision sports is assumed to indicate a reduction in verbal and analytic processes before shot release (Haufler et al., 2000). For this reason, within the current set of athletic visuospatial performance-based research, an increase in alpha power, particularly within the left hemisphere, is believed to be associated with higher degrees of skill and performance.

Although many studies have been in support of the display of neural efficiency within athletic populations, it is important to the note evidence against such findings. For instance, contradicting neural efficiency hypothesis, higher bilateral parietal ERD associated with visuospatial information processing, displayed in football players compared to non-players (Del Percio et al., 2019). Additionally, greater frontal alpha ERD has been found in professional golfers immediately before successful, compared to both novices (A. Cooke et al., 2014) and to unsuccessful putts (Babiloni et al., 2008; A. Cooke et al., 2014), and after unsuccessful putts compared to controls (Cooke et al., 2015). Greater frontal alpha ERD was also displayed in sports such as karate and fencing, comparing novices and experts (Del Percio et al., 2007). These findings were attributed to an enhancement in the recruitment of externally derived visual cues as a means of maintaining states of equilibrium (Del Percio et al., 2007), therefore suggesting greater neural involvement was required to execute the task at hand. Although an array of findings in aiming sports suggest neural efficiency, it is important to note that the targeting sports and overall visuomotor skills cannot fully act as a generalization for all sporting domains. Rather, such studies act to support an overarching representation of tasks with high visuospatial processing demands. For this reason, the neural efficiency hypothesis may not fully account for the re-organization of psychomotor systems in all expert motor-based/athletic domains, but rather may act as a tool in order to support the skillsets required to execute particular tasks within motor-based domains, such as visuomotor cognition in visual aiming tasks in order to support sports requiring target shots.

3.3. Moderating variables impacting neural indices for psychomotor performance

Although a negative relationship between neural recruitment and psychomotor task performance has been demonstrated in early research, more recent studies have identified moderating variables to impact such neuronal patterns. For instance, within motor-based domains, influencing variables such as side of body in which the movement is performed, the hemisphere evaluated, and form of athletic domain, are thought to influence neuronal activity (Del Percio et al., 2008). Furthermore, an inverse relationship between intelligence and brain activation have also been shown to rely on sex (Dunst et al., 2013; A. C. Neubauer et al., 2005, 2006; A. C. Neubauer & Fink, 2003), degree of expertise (i.e., whether in state of learning or not; Grabner et al., 2006), stability of visual information flux (Del Percio et al., 2008), brain area

investigated (Jaušovec & Jaušovec, 2004), as well as the difficulty/complexity of task (Doppelmayr, Klimesch, Sauseng, et al., 2005; A. C. Neubauer et al., 2006). This section will break down the literature revolving moderating variables which impact neuronal detection associated with psychomotor performance.

Source localization. Neuroimaging-based topographical evaluation provides insight on net distribution of activity within the cortex associated neural modulation, e.g., during cognitive states and task-specific processing mechanisms (Smith et al., 1999). Simply put, the region in the brain in which frequencies are detected, provides insight on the functions associated with detected oscillatory rhythms. For instance, within alpha rhythmic activity, sleep spindle alpha-oscillations originate from the thalamus, the mu-rhythm (8–12 Hz) motor function from central sulcus, and visual alpha EEG in perceptual functions is said to derive from occipital lobes (Gonçalves et al., 2006). For this reason, as alpha oscillations within the brain derive from distinct cortical areas, source locations associated with task-specific cognitive processing act to support the characterization and understanding of local frequency band distribution.

With cerebral cortex organization and network effectiveness measurably related to efficiency of cognitive function (Leisman, Braun-Benjamin, et al., 2014; Leisman, Rojas, et al., 2014), neuroimaging studies have shown that for neocortical regions which are not required for task execution, associated alpha activation progressively decline during task performance (Haier, Siegel, MacLachlan, et al., 1992; Jenkins, et al., 1994; Raichle et al., 1994; Seitz et al., 1990; Warren et al., 1984). It is important to reiterate how, although 'idling rhythms' indicate a lack of information is processing and/or the resting of cortical regions (Pfurtscheller et al., 1996), increases in frequency powers may additionally reflect active inhibition of task-irrelevant brain circuits (Cooper et al., 2003; Gallicchio et al., 2017; Jensen, 2002; Klimesch, Doppelmayr, et al., 1999; Raichle et al., 1994; Seitz et al., 1990; Warren et al., 1984). For instance, both in cognitive and motor tasks, ERSs are observed in brain regions which are irrelevant to task execution, and therefore are proposed to be involved in the inhibition of cognitive functions that are not directly related to the execution of the task being performed. Examples of this are how ERSs have been found in the visual cortex during execution of a motor task and in sensorimotor areas during reading (Pfurtscheller, 1992), as well as have been involved in the processing of interfering information during working memory tasks (Klimesch et al., 2007). Furthermore, as found with practice in golf putts, the selective inhibition of task-irrelevant cortical regions was also found to be concurrent with greater activation in task-relevant regions, which acted to support the manifestation of psychomotor efficiency with training (Gallicchio et al., 2017).

As network efficiency is suggested to play an essential part of task execution, the fewer brain regions necessary to execute the task renders neural processing of greater efficiency (Lotan et al., 2016). For this reason, cortical efficiency may not merely reflect a decrease in global cortical usage, but rather the reallocation of resources away from irrelevant networks to more relevant brain circuitry for the task at hand (e.g., Alperin et al., 2005; Falkmer & Gregersen, 2005; Gilchrist, 2015). For instance, although high frontal ERD (i.e., greater activation in regions associated with executive planning and decision making; Otero & Barker, 2014) has been associated with lower cognitive performance, high parieto-occipital ERD (i.e., higher activation in regions dedicated to visual perception and spatial planning; Marusic et al., 2021) has been associated with high cognitive performance (Jaušovec & Jaušovec, 2004). Such results support the idea of cortical resources being reallocated from irrelevant circuitry to regions of more critical functional processing for the individual to perform the task. This means that during psychomotor task execution, not only should individualized processing requirements be account for, but also should changes in relative relevant and irrelevant circuitry. As a result, although higher degrees of cognitive and motor performance may associate with widespread decreased in neuronal activation, regional investigation of activation may be critical

to differentiate variation in allocated resources displayed by experts, as compared to those who are novices within a particular domain.

Task difficulty. Although neural efficiency may be said to hold true for easier tasks, the reverse has been observed for tasks of higher difficulty (Doppelmayr, Klimesch, Hödlmoser, et al., 2005). This therefore renders task complexity as an essential moderating variable for the efficiency and effective allocation of neuronal resources. For instance, increased task difficulty elicits higher neural activation during cognitive tasks within occipital-temporal regions (Preusse et al., 2011) and in right inferior parietal and frontal regions (Lipp et al., 2012; Rypma et al., 2002). Further, increased lateral pre-frontal cortex (PFC) activation was found to increase with task difficulty in higher performing individuals, with minimal increase in difficulty eliciting similar activation in lower performing individuals (Rypma et al., 2002). This indicates that compared to lower performing individual (i.e., those of lower performance markers and/or novices), higher performing individuals preempt the neural investment required to execute a task of higher demand. For this reason, neural efficiency has been proposed to be the ability-dependent neural adaption in the brain, which acts in respect of task demands (Dunst et al., 2014).

Interestingly, individually perceived task difficulty has not been found to elicit differences in neural activation associated with task performance, only task performance reliant on uniformly set difficulty levels has (i.e., same sample-based; Dunst et al., 2014). As person-specific task difficulty is reliant on individual abilities, this indicates that the same task may be perceived as easier for individuals with greater cognitive abilities. Consequentially, lower performing individuals may anticipate their task-related disadvantage and thus, invest less neuronal resources (i.e., effort) to perform a task (Larson et al., 1995). Further, Jaušovec & Jaušovec (2004) found high frontal ERD to associated with lower cognitive performance, yet high parieto-occipital ERD to associate with high cognitive performance. As frontal regions are associated with executive planning and decision making (Otero & Barker, 2014) and parieto-occipital regions are thought to account for visual perception and spatial planning (Marusic et al., 2021), such findings suggest that interindividual processing requirements relating to perceived task difficulty, exist in accordance with source localized processing mechanisms. Consequently, perceived task difficulty can be said to be responsible for individual brain activation-based differences which underpins cognitive abilities (such as fluid intelligence; Dunst et al., 2014), indicating that neural efficiency is a function of both intelligence and sample-based task difficulty and demands.

Effort, motivation, and intention. As the anticipation of task-related advantage (or disadvantage, for that matter) can impact an individual's investment of neuronal resources used to perform a task (Larson et al., 1995), effort, motivation, and intention are therefore critically interwoven into perceived task difficulty regarding its impact on task performance. Historically, according to Brehm's theory, effort expenditure can be thought to depend on task difficulty and motivation, whereby the higher the difficulty of the task, the higher the investment of effort required (Brehm & Self, 1989). However, according to Yerkes & Dodson's law, the investment in effort (i.e., arousal) only persists up to motivations at moderate intensities and is accompanied by a performance decline above a certain point (as depicted by an inverted U-shaped function displayed in Fig. 4; Yerkes & Dodson, 1908). For instance, within tasks of higher complexity, higher recruitment of cortical resources is observed, which suggests a positive correlation between cortical activation and performance abilities (e.g., cognitive performance, which was found in frontal regions; Neubauer & Fink, 2009). For this reason, neural efficiency is likely associated with tasks of low to moderate task difficulty (i.e., requiring low levels of arousal), both objective and subjectively, and during novel cognitive tasks or after sufficient practice (A. C. Neubauer & Fink, 2009).

In terms of relative economy of effort, dynamic psychomotor performance may be achieved with high degrees of cortical investment, although only involving relevant forms of processing (Salamone et al.,

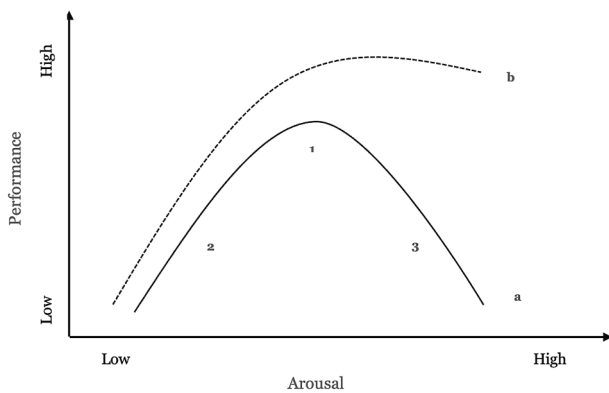


Fig. 4. A schematic outline of the relationship between performance and arousal levels for a) simple tasks (e.g., requiring focused attention, as per the Yerkes & Dodson law; [Yerkes & Dodson, 1908](#)) and b) difficult tasks (e.g., involving divided intention and multitasking, decision making, and/or working memory). On graph a., region 1. represents states of increased performance with increasing arousal; region 2 represents the state of arousal in which peak performance is achieved; region 3 represents the states of arousal in which result in a decline in performance. Graph was adapted from [Whiting et al. \(2021\)](#).

2016, 2018). As relative economy of effort is thought to be sustained within experts, assuming that experts are possibly more engaged with a task, this view may be perceived as a saving of unnecessary resource allocation, and thus, the inhibition of irrelevant neural pathways ([Haufler et al., 2000](#)). The neurophysiological explanations of relative economy of effort describe an increase in alpha power with inhibition of irrelevant neural resources, while other neural processing is actively engaged ([Klimesch, Doppelmayr, et al., 1999](#)). This indicates that neurobiology underpinning cognitive abilities adjusts with effort, in order to support the development of efficient mechanism to support task execution ([Neubauer & Fink, 2009](#)).

Connected to this, intention is a behavioural variable which impacts EEG alpha-power reactivity. Intention can be said to replace environmentally derived visual attention, and thus control task execution via subconscious automatic mechanisms ([Shaw, 1996](#)). Further, prior to skill execution, neural pathways associated with intention operate such that optimal motor output selections are favored, whereby less optimal courses of action are filtered out ([Jeannerod, 1994, 1997](#)). For instance, increases in visuomotor task performance have been attributed to suppressions in visual attention, and thus, less cortical effort to process necessary information to perform the task, as controlled by the mechanism of intention ([Loze et al., 2001](#)). This particularly holds true for highly trained and highly performing individuals, as only well learnt actions have the ability to support the automaticity associated with internal action-based neurocognitive strategies (i.e., neural adaptations associated with the long-term practice of and/or execution of a task; [Shaw, 1996; Wang et al., 2020](#)). In other words, the intention to perform a task acts to support the training required to develop effective neurocognitive strategies and adaptations of neural pathways, which support more efficient task execution ([Mazzoni & Krakauer, 2006; Taylor & Ivry, 2011](#)). For this reason, intention lends itself as a critical element for neural efficiency.

Training, practice, and familiarity. Psychomotor execution of unfamiliar tasks involves considerable cognitive effort, due to lack of strategized coordination and decision making involved in executing the movement ([Cross, 1967; Hodges et al., 2006; Lee et al., 1994](#)). Such processes involve the trialing of untested response strategies, which are used in an elimination process to determine the most suitable means of task execution. The development of internal self-instruction processes involves an electrochemical reorganization of neural communication, which occurs amongst both cortical and subcortical neurons. As a result, the plasticity of the nervous system facilitates a decrease in neuronal

investment for the skill development of low order tasks, resulting in a decrease in both mechanisms of conscious regulatory and executory control ([Badgaiyan, 2000; Cohen, 2014; Hatfield et al., 2020; Smith et al., 1999](#)).

Although the intention to perform a psychomotor task at a high degree of expertise may be present, without training and practice required within skill acquisition, task-specific neurocognitive strategies which facilitate task-related self-instructions are likely to not be achieved ([Abernethy & Russell, 1987; Dorothy V. Harris & Bette L. Harris, 1984; Robert N. Singer et al., 1993; Smith et al., 1999](#)). From a neurophysiological standpoint, practice induces an increase in stability in motor-based processing, which derived from a decrease in required retrieval from working memory processes. Subsequently, a reduction in interference from less relevant synaptic transmission, and thus, the reductions of signal from sources of competing pathways, is achieved ([Hatfield et al., 2020](#)). For this reason, sustained practice can be said to increase the familiarity of a task, which facilitate towards an effective formulation of self-internalized strategies. This thereby reduces the uncertainty involved in the execution of the task, and thus, support the decrease in relative complexity and cognitive effort (i.e., making the task execution more autonomous in nature; [Cohen, 2014; Fitts, 1967; Hatfield et al., 2020](#)). Therefore, practically speaking, training and practice can be said to support the increase in consistency of behavioral output, resulting in psychomotor efficiency within psychomotor professions (such as sports; [Haufler et al., 2000](#)).

The modification and optimization of internal model is accompanied by a decrease in the requirement of feedback, along with an increase in reliance on procedural memory, as stated within the schema theory for motor learning ([Smith et al., 1999](#)). In support of this model, motor-based domains have also elicited evidence of neuronal advantage from training, such as violin training being found to result in a task-specific functional reorganization, as existing in the form of right-dominant hemispheric asymmetries ([Schwenkreis et al., 2007](#)). Sports requiring quick and efficient integration of unwarned visual information (e.g., boxing, karate, etc.) are also said to benefit from repetitive training in order to induce higher neuronal certainty ([Del Percio et al., 2008](#)). Although perceptual training can be effective for both athletes ([Farrow & Abernethy, 2002; Murgia et al., 2014](#)) and non-athletes ([Ryu et al., 2013; Savelsbergh et al., 2010](#)) in a shorter time scales (i.e., weeks or months), from a behavioral standpoint, more effective task-related organization of neural networks stem from extensive practice over long periods of time ([Babiloni, Marzano, Infarinato, et al., 2010; Del Percio et al., 2008](#)). For this reason, long-term psychomotor training can be thought to support the development of task-related efficient organization of neural networks. However, it should be emphasized that such functional reorganization is task-specific, rather than a generalized mechanism for all sensorimotor processes ([Guo et al., 2017](#)).

Within cognitive domains, reduced selective event-related cortical activation has been found to be associated with highly trained individuals, acting in support of neural efficiency ([Grabner et al., 2004; A. C. Neubauer et al., 2004](#)). More specifically, less intense ERD was found to be lower in highly trained experts compared to non-experts during a short-term memory task ([Grabner et al., 2006](#)). Interestingly, a reduction in ERD has also been found to associate with the automaticity of task execution achieved from explicit learning ([Gehring et al., 2018; Pfurtscheller & Lopes da Silva, 1999](#)). Further, when comparing cortical investments pre-test and post cognitive tests, negative correlations were found with intelligence, whereby the higher the mental ability, the larger the decrease in the amount of cortical activation ([A. C. Neubauer et al., 2004](#)). As negative intelligence-activation correlation was observed only after the training (i.e., in the post-test and not in the pre-test), intelligence-related individual differences in mechanisms associating with neural efficiency, can be partially accounted for by mechanisms revolving around task-specific training ([A. C. Neubauer et al., 2004](#)).

Neurophysiological indices of practice indicate that practiced

performance-based executions are predominantly presented as decreases in frontal cortex areas and increase in task-relevant brain regions, both for cognitive and sensorimotor processes (Babiloni, Marzano, Infarinato, et al., 2010; Hardwick et al., 2013; A. M. C. Kelly & Garavan, 2005). For instance, athletes have been shown to exhibit greater cortical activation in task-sensitive areas, such as motor regions, when performing a familiar task compared to an unfamiliar/less familiar task (Calvo-Merino et al., 2005, 2006; Lyons et al., 2010; Woods et al., 2014). As decreased event-related cortical activity (i.e., suppression of cognitive processing) has been identified both along learning phases and during trained motor tasks (Kerick et al., 2001, 2004), training therefore has been said to facilitate decreases in activity in motor regions of the brain (i.e., from pre- to post-training; Haufier et al., 2000; Jäncke et al., 2006; Koeneke et al., 2006). Interestingly, the reorganization of activation for practiced-based performance has not only been shown to include motor regions, but also ‘mirror’ systems, indicating that those who are trained potentially experience both visual and motorically-based processing advantages (Calvo-Merino et al., 2005, 2006).

Since long-term training facilitates the development of a focused and efficient organization of task-related neural networks within psychomotor domains (e.g., in athletes; Milton et al., 2007), this indicates that source location of activity acts as a salient component of selective neuronal reorganization. For instance, the learning of a motor sequence has been found to be accompanied by an enhanced alpha ERD in cortical regions responsible for motor learning (i.e., in sensorimotor areas, such as over the contralateral central regions), which decreases after the task has been learned (Zhuang et al., 1997). Although this has been found, e.g., using simple finger movement sequences (Zhuang et al., 1997), movements of greater complexity may have adaptational requirements involving more sophisticated cognitive processes, such as those pertaining to refinements of more dynamic motor movements (Kozioł et al., 2014; Leisman, Braun-Benjamin, et al., 2014; Melillo & Leisman, 2010; Schack, 2004; Schmähmann, 1996). Therefore, although neural efficiency may lend itself to the learning of simple motor tasks, the neuroadaptation associated with training involved in motor executions of greater complexity may require a model of greater specificity and/or intricacy.

Attention and automaticity. As phase-synchronized rhythmic activity across long-range connections is influenced by locally synchronized neuronal groups, this means that both local and long-range spatial scales impact selective neuronal modulation (S. Zhang et al., 2014). Specifically, selectively synchronizing neuronal responses pertaining to relevant sensory cues, allows for information to be more effectively processed within dynamic parameters (Womelsdorf & Fries, 2007). This means that attention supports adaptive neuronal modulation, and thus enhances both local spatial (Reynolds & Chelazzi, 2004) and featural (Maunsell & Treue, 2006) attunement of attended sensory input. Interestingly, synchronization strength of neural connections may elicit a selective advantage for memory formation (Osipova et al., 2006; Pesaran et al., 2002; Sederberg et al., n.d.; Xin et al., 2011), as well as predict behavioural response speed (Gonzalez Andino et al., 2004; Kaiser et al., 2006; Womelsdorf et al., 2006) and perceptual accuracy (Gross et al., 2004; Linkenkaer-Hansen et al., 2004; Nakatani et al., 2005; Tallon-Baudry et al., 2004). Therefore, perceptual accuracy and behavioural efficiency functionally influence the strength of synchronization, which both act as functions of attention (Womelsdorf & Fries, 2007). In other words, local neuronal networks functionally fluctuate in attunement with attended stimuli, whereby the strength of synchronization are functionally reliant on attention (Miller & D’Esposito, 2005).

Relatedly, it is suggested that alpha-band synchronization may have an active role in preventing effective local neuronal processing (Womelsdorf & Fries, 2007). In other words, higher degrees of performance are accompanied by higher consistency of the involved cognitive and motor processes, likely due to less interference of irrelevant forms of processing (Konttinen et al., 1999). This derives from how neuronal groups which process stimuli from unattended source locations (i.e.,

distractions/irrelevant information) were found to selectively enhance alpha-band activity (S. P. Kelly et al., 2006; Yamagishi et al., 2003). As local alpha attenuation derives from functions of the dorsal attention network (which selectively disrupts alertness-related suppression; Sadaghiani et al., 2010), active neural modulation in the form of increased alpha power, are thought suppress potentially distracting sensory information (Bowman et al., 2017; Foxe, 2011; Payne & Sekuler, 2014). Further, as the enhancement of neuronal recruitment of pathways pertaining to relevant information is selectively synchronized via attention, it makes sense that a reduction in alpha ERS is associated with attentional processing (Bauer et al., 2006; Fries et al., 2001; Müller & Keil, 2004; Palva et al., 2005; Pesaran et al., 2002; Yamagishi et al., 2005).

In support of the relationship between the alpha band and attention, high ERD has been associated with the increased effort and attention required in lower IQ (Grabner et al., 2004; A. Neubauer et al., 1995; A. C. Neubauer et al., 1999) and elderly patients (Defebvre et al., 1996; Johari & Behroozmand, 2020), indicating that functions of attention indeed impact changes in cortical activity. Further, increases in task complexity, and thus tasks requiring greater degrees of attention, are associated with relative increases in ERD (Boiten et al., 1992; Dujardin et al., 1993). Particularly, visual external attention has been found to cause significant parietal-occipital alpha ERD, where a direct correspondence between degree alpha decrease was found with an increase in arithmetic demand (Magosso et al., 2019). Interestingly, external attention is not only accompanied by decreased alpha power in occipital regions, but also corresponds with increases in excitability of visual cortex, which facilitates sensory processing (Mo et al., 2013). Moreover, both visual stimulation (Niedermeyer, 1997; Romei et al., 2008) and attention (Sauseng, Klimesch, Stadler, et al., 2005) are thought to be associated with alpha activity detected in the posterior regions of the brain. Thus, increases in activity (i.e., decreases in powers) in such regions can be thought to be mediated by high degrees of focus. Overall, alpha activity is decreased in task-relevant cortices during externally oriented attention, whereas increased alpha activity associates with decreased level of visual processing and poorer behavioral performance (Mo et al., 2013).

Further, as the sequential actions involved in both learning and executing psychomotor tasks are facilitated by executive functions and automaticity (Keele et al., 2003; Nixon & Passingham, 2000), automaticity thereby plays a dominant role in high degrees of psychomotor performance. As novel tasks are considered to be attentionally demanding (Smith et al., 1999), a decrease in novelty of a task (e.g., due to training) can be thought to progressively decrease the neuronal tax associated with adaptations in cortical processes. In other words, automaticity encapsulates states of effective task execution, and is involved in the process of tasks becoming more routine and requiring less internal deliberation. Thus, the decrease neuronal recruitment of those who are highly trained compared to those who are unpractised and/or are in a phase of skill acquisition, supports neurophysiological models such as the ‘neural efficiency’ hypothesis (Abernethy & Russell, 1987; Allard, 1993; Ericsson & Smith, 1992; Holyoak, 1991; Robert N. Singer et al., 1993). This indicates that a more efficient and effective cortical processing is postulated to facilitate higher degrees of task execution, and therefore, degree of attentional demands associated to states of automaticity, can be said to be a moderating variable which requires consideration when evaluating neural efficiency markers relating to performance within psychomotor domains (see Table 2 for summary).

3.4. Alpha activity and the default mode network

Just as the physiological consequence of eyes being opened involves the reorganization of selective brain activity in the form of suppressed alpha power (i.e., the enhancement of alpha activity; Berger, 1929; Moosmann et al., 2003), the act of eyes closing also suppresses functional connectivity within the Default Mode Network (DMN; Yan et al.,

Table 2
Outlines a summary of the moderating variables impacting the psychomotor neural efficiency model, as well as the consequences of these variables.

Moderating Variable	Key Points	Consequences
Source localization	<ul style="list-style-type: none">• The region in which oscillatory frequencies are detected provide insight on the functions of detected activity.• Decreases in cortical activation are observed in irrelevant regions of the brain during psychomotor task execution.	<ul style="list-style-type: none">• Cortical efficiency may not merely reflect a decrease in global cortical usage, but rather the reallocation of resources away from irrelevant networks to more relevant brain circuitry for the task at hand.• Both individualized processing requirements and changes in relative relevant and irrelevant circuitry, should be accounted for during psychomotor task execution.
Task difficulty	<ul style="list-style-type: none">• Neural efficiency may hold true for easier tasks, although the reverse has been observed for tasks of higher difficulty.• Perceived task difficulty is responsible for individual brain activation-based differences, which underpins cognitive abilities.	<ul style="list-style-type: none">• Neural efficiency is a function of both intelligence and sample-based task difficulty and demands.
Effort, motivation, and intention	<ul style="list-style-type: none">• Relative economy of effort describes an increase in alpha power with inhibition of irrelevant neural resources.• The intention to perform a task acts to support the training required to develop effective neurocognitive strategies and adaptations of neural pathways.	<ul style="list-style-type: none">• The relative economy of effort of experts can be viewed as a saving of unnecessary resource allocation, and thus, the inhibition of irrelevant neural pathways (Haufler et al., 2000).
Practice, training, and familiarity	<ul style="list-style-type: none">• Sustained practice increases the familiarity of a task, which facilitates the effective formulation of self-internalized strategies.• Training and practice support the increase in consistency of behavioral output, resulting in psychomotor efficiency within psychomotor professions.• Practiced performance-based executions are predominantly presented as decreases in frontal cortex areas and increase in task-relevant brain regions.	<ul style="list-style-type: none">• Long-term psychomotor training supports the development of task-related efficient organization of neural networks.• Psychomotor-based functional reorganization associated with expertise is task-specific, rather than a generalized mechanism for all sensorimotor processes (Guo et al., 2017).• Although neural efficiency may lend itself to the learning of simple motor tasks, the neuroadaptation associated with training involved in motor executions of greater complexity may require a model of greater specificity.
Attention and automaticity	<ul style="list-style-type: none">• Functions of attention impact changes in cortical activity.• Reduction in alpha ERS are associated with attentional processing (Bauer et al., 2006; Fries et al., 2001; Müller & Keil, 2004; Palva et al., 2005; Pesaran et al., 2002; Yamagishi et al., 2005).• Tasks requiring higher degrees of attention are	<ul style="list-style-type: none">• More efficient and effective cortical processing, and thus, automaticity, is postulated to facilitate higher degrees of task execution.• Degree of attentional demands associated to states of automaticity, is a moderating variable which requires consideration when evaluating

Moderating Variable	Key Points	Consequences
	<ul style="list-style-type: none">• associated with relative increases in ERD (Boiten et al., 1992; Dujardin et al., 1993).• Alpha activity is decreased in task-relevant cortices during externally oriented attention.• Increased alpha activity is associates with decreased level of visual processing and poorer behavioral performance (Mo et al., 2013).	psychomotor neural efficiency markers.

n.d.). Interestingly, eyes opening has resulted in significant reduction in alpha-related hemodynamic responses (i.e., hemodynamic correlates of EEG-based alpha activity; de Munck et al., 2007) in multiple brain regions, such as those in the DMN (Wu et al., 2010). The DMN is a cortical and subcortical network system which emits a strong low-frequency oscillations during states of limited multimodal sensory input (e.g., lying quietly with eyes-closed: Chen et al., 2008). This ‘default’ state of the human brain therefore activates during states of internal mental-state processes, including interception, self-referential processing, memory retrieval, or future projections, and deactivates during engaging extrinsic tasks (Raichle et al., 2001; Raichle & Snyder, 2007). Simply put, the DMN is enhanced during rest and decreased in activity during task engagement, therefore is also referred to as the task-negative network (Fox et al., 2005; Gusnard & Raichle, 2001; Shulman et al., 1997). On average, the DMN is deactivated during active engagement in tasks requiring high cognitive demand (Buckner et al., 2008), whereby greater suppression in DMN activity is associated with increased activation of the sensory cortices (Greicius & Menon, 2004). Further, lower DMN activity has been associated with higher degrees visual cortical excitability, which act to assist the facilitation of stimulus processing (Mo et al., 2013). This means that activation (or, less suppression) of the task-negative network during task execution may be indicative a decreased reliance on external stimuli.

As per the ‘introspection’ hypothesis, the DMN is theorized to play a role in introspection, mind wandering, or daydreaming during resting states (Mason et al., 2007), although the DMN may also regulate vigilance, monitor external stimuli, and focus attention (i.e., as per the ‘sentinel’ hypothesis; Gilbert et al., 2007; Raichle et al., 1996). Interestingly, both externally derived attention and an increase in sensory input processing are accompanied by a suppressed alpha power and DMN activity (Foxe et al., 1998; Greicius & Menon, 2004; McKiernan et al., 2003; Thut et al., 2006). This suggests that a plausible relationship may exists between the two. Furthermore, alpha power and DMN activity are both found to heighten preceding momentary lapses in visual attention (Eichele et al., 2008; O’Connell et al., 2009; Weissman et al., 2006). The positive relationship suspected to exist between alpha power and DMN activity, suggests that introspective processes may be ‘protected’ from external interference (Mo et al., 2013), rendering both alpha and DMN activity as key elements for task execution. This suggests that higher alpha power (e.g., ERS or less ERD) and less suppression of the DMN may be indicative of less cortical investment while performing a task, and thus, increased cortical efficiency.

Although some findings suggest that sustained decreased EEG activity during tasks may reflect depression in DMN activity (e.g.: Ossandón et al., 2011), the relationship between the DMN and alpha activity is conflicting. For instance, subnetworks of the DMN have been shown to have opposite correlations with alpha EEG power, which may indicate a separate relationship of EEG-based indices for different functions of the DMN (i.e., introspection vs sentinel; Bowman et al.,

2017). Such findings may explain the inconsistencies in previous findings examining the relationship between the DMN and alpha rhythms, and additionally suggest that overlapping regions of the DMN may be involved in the switch between introspection and sentinel-based functions. Overall, correlative patterns of EEG activity and the DMN indicate that EEG alpha band may act as insight for sub cortical networks, such as the DMN, although further evidence is needed to support this claim (Mo et al., 2013).

3.5. Practical application and future work

The EEG. The EEG is a well-documented non-invasive brain imaging techniques (Berger, 1929), which has been shown to be sensitive to practice-related changes in the neuronal resource allocation and attentional demands associated with both task-specific skill acquisition and execution (Smith et al., 1999). The EEG provides dynamic assessment of the brain-based activity at a fairly low cost, making it a relatively accessible monitoring system compared to alternative neuroimaging techniques (i.e., Functional Magnetic Resonance Imaging (fMRI)). This renders the EEG as advantageous in applicational use, specifically for its ability to provide conceptual framework of the relationship between anatomy, physiology, behavioral studies, neuropharmacology, engineering, and physics (Nowack, 1995). Therefore, the EEG lends itself to varied experimental designs, scales, and brain states relating to theories underlying cognitive processing (Niedermeyer & Lopes da Silva, 1982), making it a highly versatile measurement tool as whole.

Further, as presented within this review, task-specific neuro-modulation associated with the development of neurocognitive strategies may be investigated using EEG-based indices and markers such as ERD/ERS evaluation paired with topographical distribution. This means that the accompanying changes in EEG signals that may reflect neural reorganization associating with skill acquisition, can be detected on both global and local (i.e., regional activity distribution) scale. For this reason, neuroimaging techniques, such as the EEG, are suggested for the use of monitoring the neural adaptation processes occurring as a consequence of tasks performance, as well as learning bouts (Smith et al., 1999). The EEG therefore offers a potential feasible approach for online assessment of brain networks, through the monitoring of characteristic dynamic responses to task requirements (Morrone & Minini, 2023).

Although the EEG offers great potential for practical use within both cognitive and motor-based domains, moderating variables impacting detectable neural indices require consideration. For instance, although the EEG has high temporal resolution, it also has relatively poor spatial resolution (e.g., compared to fMRI), meaning that it is unable to provide direct access to sub cortical active deep brain. As the volume conduction properties of EEG measurements involves detected activity being predominately detected by surface electrode and thus from cortical structures, this therefore makes localization of EEG sources overall difficult (DiFrancesco et al., 2008). Even so, the EEG offers the potential to detect underlying neural pathways through correlated neuronal indices of subcortical networks (i.e., such as subcortical structures within the DMN), making it a powerful neuroimaging technique with a wide range of applications. As presented within this review, such application may involve the detecting and monitoring of the neural adaptations in the form of selective cortical reorganization, accompanying both skill acquisition within psychomotor domains.

Potential for adopting the neural efficiency hypothesis. Considering that the involvement of sensorimotor cortical systems may be more complex than that explained by the “neural efficiency” hypothesis in the elite population (e.g., athletic; Del Percio et al., 2008), the idea of neural efficiency may be adopted as long as impacting factors are considered. As spatially selective events or task-related cortical activation may reflect other mechanisms underlying task features and moderating variables, it has been proposed that in order to enrich current neurophysiological models associated with the functionality of alpha activity

(i.e., ERD/ERS, coherence, ERP, etc.; Del Percio et al., 2019), psychometric tests (such as ‘situational awareness’) will have to be implemented alongside current investigations. It is also proposed that benefit would be made from testing neural modulation of alongside other frequency bands for neural efficiency, such the beta (13–35 Hz) and gamma (>35 Hz) bands. As a result, such methods offer a means to foundational information revolving neural correlates of mental processes in specialized populations, such as athletes during sporting performances (Gallicchio et al., 2016; Zhu et al., 2011).

4. Conclusion

Within the present article, electroencephalography-based neurophysiological indices encapsulating heightened psychomotor performance were explored as a means of characterizing fundamental processes underlying efficient psychometric performance. The neural efficiency model was evaluated in terms of alpha-wave-based selective cortical processes, initially explored pertaining to cognitive and motor domains independently. Doing so supported the encapsulation of task-related neuronal adaptive requirements for enhanced psychomotor performance associating with the neural efficiency model. Moderating variables impacting the practical application of such neuropsychological model, were investigated. As a result, this review aimed to provide insight on detectable task-related modulation involved developed neurocognitive strategies which support heightened dynamic psychomotor performance. Such knowledge is proposed to provide a foundation for the subsequent neuromodulation research, specifically for the implementation within practical settings (such as sports or military operational settings).

CRedit authorship contribution statement

Jazmin M. Morrone: Conceptualization, Writing – original draft, Writing – review & editing. **Charles R. Pedlar:** Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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