The cortical aftereffects of dynamic handgrip and the role of the electroencephalographic alpha and theta bands before and during visuomotor performance

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Overview

In the present doctoral dissertation, the cortical aftereffects of *dynamic handgrip* (Kluess et al., 2000; Napadow et al., 2008) and their repercussion on visuomotor performance under pressure were investigated. Handgrip exercises, also referred as hand-clenching (Propper, 2013) or hand-contractions (Harmon-Jones, 2006; Beckmann et al., 2013), consist on vigorously pressing a device, commonly a soft rubber ball, with one hand for around half-minute. The contractions can be either static (Sander et al, 2010) or dynamic (Kluess, 2000; Napadow et al., 2008; Meleis et al., 1982), which show similar cortical activation patterns during execution (Liu et al., 2003). These manipulations have been used to induce varied behavioral after-effects, enhancing performance on tasks assumed to rely strongly on the brain hemisphere contralateral to the hand previously used. For example, memory encoding tasks mostly dependent on the left hemisphere, after right handgrip (Propper, 2013); or a word association-creativity test, largely reliant on the right hemisphere, after left handgrip (Goldstein et al., 2010).

Beckmann et al. (2013) utilized left-dynamic handgrip to prevent visuomotor skill failure in experienced athletes performing under pressure. Research supports that skilled visuomotor performance relies on right parietal activation (Milton et al., 2004; van Mier et al., 1998; Salazar et al., 1990) and is disrupted by activation of the left hemisphere (Salazar, 1990). In the experiments by Beckmann et al., athletes that executed left dynamic-handgrip (inducing right hemisphere dominance) were often resistant to skill failure under pressure, while those that executed right dynamic handgrip were not.

Using electroencephalogram (EEG), Harmon-Jones (2006) and Peterson et al. (2008) compared two groups that executed left or right static handgrip, and observed greater relative hemispheric activation of the contralateral hemisphere in each group, not only in motor regions, but over extended cortical areas. Based on those findings, it has been proposed that the behavioral aftereffects of handgrip result from the dominance of one brain hemisphere induced during contractions (Beckmann et al., 2013; Propper et al., 2013; Goldstein et al., 2010). However, the cortical state after handgrip is terminated has not been directly assessed to investigate if the allegedly induced hemispheric dominance persists after contractions, and for how long. An alternative possibility based on studies of brain stimulation post-exercise is that handgrip induces a state of generalized reduced cortical activity after termination (Zanette et al., 1995; Bäumer et al., 2002), which may facilitate further task engagement after reducing task-incompatible cortical activity (Collins et al., 1990; Kapur, 1996; Miller et al., 2000; Hatfield et al., 2004).

In the current thesis, the first aim was to clarify the cortical aftereffects of dynamic handgrip as used by Beckmann et al. (2013). In the first study (Cross-Villasana et al., 2015), the EEG alpha band (8-12 Hz) was used as an indicator of cortical activity to examine the long term effects produced by dynamic handgrip of each hand. Right handed participants executed left and right dynamic handgrip for 45 seconds, a baseline measurement before contractions, a measurement after contractions, and a 2 minute break between the procedure for each hand were included. The main result showed a bilateral activation over sensorimotor areas during handgrip, and a significant enhancement of alpha amplitudes above baseline only after left handgrip, which indicate a reduction of cortical activity. Unlike Harmon-Jones (2006), no modulations of activation asymmetry between the hemispheres were observed during or after the handgrip periods. These observations were persistent with a linked mastoids, surface laplacian, and average reference scheme. Based on these results, it is argued that the behavioral effects of handgrip likely result from a state of generalized reduced cortical activity greater after left than after right contractions, rather than dominant activity of one hemisphere.

The first study also replicated classical findings from EEG event-related studies of human movement. For the average of the whole handgrip period of any hand, a reduction of activity over the occipital cortex simultaneous to the sensorimotor activation was observed, analogous to that reported by Pfurtscheller and Lopes da Silva (1999) when averaging multiple single contractions. On the first second after contractions, a rebound of the upper alpha band (10-12 Hz; also known as Mu rhythm) was observed, similar to that reported by Pfurtscheller and Lopes da Silva (1999) when averaging multiple trials. This rebound implies the onset of inhibitory mechanisms (Pfurtscheller & Lopes da Silva, 1999) and it was greater for the left than for the right hand. It is argued that these two inhibitions extend towards the period after contractions and produce reduction of activity reported in the main result.

On the second study, the aim was to test the repercussion of the cortical aftereffects of dynamic handgrip on visuomotor performance under pressure. For this purpose, a custom single-player version of the videogame “Pong” (Rebert & Low, 1978; Rebert et al., 1984) was developed as an EEG-suitable task which assimilates the fluid nature of sportive performance from Beckmann et al (2013). Skill break down would disrupt the right parietal activations necessary for visuomotor performance, and left dynamic handgrip before performance might prevent this disruption. Right handed participants first trained the task, on a following day, they played 15 stress-free trials, and 15 trials with stress induction through video recording (Jackson et al., 2006) and through pressure to perform (Baumeister, 1984). Trial duration was assessed. Before stress, three different groups performed either left, right or no dynamic handgrip. Stress did not disrupt trial duration of any group compared to stress-free. However, in the whole sample, the induction of right parietal dominance while playing Pong (Rebert & Low, 1978), and an increase of the EEG theta band (Rebert et al 1984) were replicated. Theta amplitudes correlated negatively with performance among participants, signaling that proficiency in the task requires reduced conscious control while performing. Alpha reactivity after eye opening was predictive of subsequent performance. Given the reliable EEG markers observed, it is concluded that Pong is a suitable laboratory task for testing visuomotor skill failure but stress induction needs to be improved.

Taken together, the results suggest that a generalized reduction of cortical activity triggered after dynamic handgrip might be responsible for its behavioural aftereffects. “Pong” provides valid EEG markers that relate to performance, hence it is a valid task to investigate visuomotor skill failure, but the stress induction method needs to be improved. Since skilled players showed smaller theta amplitudes than less skilled players, skill breakdown may be accompanied by an increase in theta.

Table of Contents

Chapter 1

Introduction: State of the art and preliminary work

1.1 BRAIN LATERALITY

Asymmetries in anatomy, physiology and function between the brain's hemispheres have been consistently observed in animal and human research (Iturria-Medina, et al., 2011; McGilchrist, 2010; Toga & Thompson, 2003). For instance, while the cortex of the left hemisphere shows a localized modular organization in its connectivity, the right cortex has greater myelination and more extended overlapping connections among areas of itself and to the rest of the brain (Iturria-Medina et al., 2011; Scheibel et al., 1985; Seldon, 1982; Allen et al., 2003; Gur et al., 1980; Tucker et al. 1986). Evidence supports that such anatomical differences help bringing particular modes of information processing to each hemisphere (Iturria-Medina et al., 2011; McGilchrist, 2010; Toga & Thompson, 2003). With its localized circuitry, the left hemisphere is better capable of serial processing, focus on details and semantic structures, and to deploy a narrow and focused type of attention; while the right hemisphere, thanks to its widespread connections is suited for parallel processing, attends the broader space and makes overall associations among stimuli (Iturria-Medina et al., 2011; McGilchrist, 2010; Gazzaniga, 2000). These processing modes make each hemisphere more suitable for certain types of stimuli and facilitate their functional specializations, with the left hemisphere specialized for highly precise linguistic, symbolic and sequential operations, and the right hemisphere proficient mostly in perceptual functions such as attentional monitoring or face recognition (Iturria-Medina et al., 2011; McGilchrist, 2010; Gazanniga, 2000). The left hemisphere is also associated with conscious executive processes and shows an intrinsic tendency for interpretation of behavior in relation to events (Nielsen et al., 2013; Gazzaniga, 2000). Many behaviors that are first carried automatically by the right hemisphere are then interpreted as a deliberate act by the left (Gazzaniga, 2000).

1.2 COMPETITION BETWEEN THE BRAIN'S HEMISPHERES AND BEHAVIORAL CONSEQUENCES

Normal task performance requires the hemispheres to keep a balanced interaction through mutual excitatory and inhibitory mechanisms (Kapur, 1996; Shimizu et al., 2002; Bloom & Hynd, 2005) mediated mainly by the corpus callosum (Meyer et al., 1995; Gazzaniga, 2000; Shimizu et al., 2002; Bloom & Hynd, 2005). With their differing processing modes, the two hemispheres tend to compete for the processing of information (Kapur, 1996; Hilgetag et al., 1999; Kobayashi et al., 2004), transmitting only the final outputs of some computations to the opposite hemisphere (Bloom & Hynd, 2005; Gazzaniga, 2000; Banich, 1998).

Unimanual tasks are an example of this complex interaction in which mutual inhibition is a prominent competitive mechanism, that allows for the movement of one hand, without mirror movements from the other (Carson, 2010; Nirkko et al., 2001; Hamzei et al., 2002). In a study using functional magnetic resonance imaging (fMRI), Allison et al. (2000) report that during the execution of complex finger sequences, contralateral activation and ipsilateral inhibition of homolog sensorimotor areas relative to the active hand took place. Similar effects were observed by Hamzei et al. (2002) during submaximal pinch-grips. Allison et al (2000) further argued that those areas that deactivate during ipsilateral movement, might not be the same ones that activate during contralateral movement. The latter suspicion was confirmed by Nirkko et al. (2001) who precisely observed that during a self-paced finger opposition task in fMRI, the simultaneous inhibition was restricted to the ipsilateral primary motor areas, but ipsilateral premotor areas showed simultaneous activation. Multiple transcranial magnetic stimulation (TMS) studies show that the activation of one motor cortex through magnetic pulses reduces the evoked motor response from a following pulse to the contralateral motor cortex within a window of 100 ms (Liepert et al., 2001; Liepert et al., 1996; Wasserman et al, 1991; Ferbert et al., 1992; Meyer et al., 1998; Chiappa et al. 1995; Taylor et al., 1995), and this effect is absent or attenuated in patients with deficiencies in the corpus callosum (Rothwell et al., 1991; Meyer et al. 1995).

Competition between the hemispheres becomes more evident when the impairment of a single hemisphere disrupts the competitive balance and produces hyper-excitability of the unaffected hemisphere, after it no longer receives contralateral inhibitory input (Shimizu et al., 2002; Hilgetag et al., 1999). Mansur et al. (2005) improved unimanual motor function in stroke patients by suppressing the unaffected hemisphere via repetitive TMS (rTMS), while Kobayashi et al. (2004) enhanced the motor performance of healthy subjects in a sequential button press task by suppressing the M1 ipsilateral to the active hand with rTMS. Oliveri et al. (1999) increased sensitivity to left hand cutaneous stimulation in right brain-damaged patients by transiently disrupting the frontal left hemisphere with single pulse TMS shortly before each stimulus. Analogous effects have been observed in the perceptual domain; in healthy subjects, attention to one side of the space can be enhanced by the momentary suppression of the ipsilateral parietal lobe via repetitive TMS (rTMS) therefore freeing the attending contralateral hemisphere from inhibitory inputs (Hilgetag, et al., 2001). Conversely, in stroke patients with hemispatial neglect, spatial attention can normalize if the healthy hemisphere gets also disrupted by a subsequent stroke (Vuilleumier et al., 1996), or if it is suppressed transiently via rTMS (Oliveri et al. 2001) so that the activation level between the two hemispheres is balanced again. In the language domain, it has been observed that people with greater bilateral representation of language have a greater tendency to stutter, and that lesions to one hemisphere in such individuals bring an end to stuttering (Kapur, 1996). According to Kapur (1996), the competition between the hemispheres when language is bilaterally represented, is eliminated after the lesion, allowing a single hemisphere to better control language without competition.

Competitive misbalance between the hemispheres can also affect complex behaviors that require higher cognitive functions. Patients with left fronto-temporal dementia, despite the loss of language and social skills, can show enhancement of previously existing artistic visual or musical abilities, or even develop them anew (Miller et al., 2000; Miller et al., 1998; Gordon, 2005). Moreover Snyder et al. (2003) report inducing artistic-like drawing skills in healthy subjects by suppressing the left anterior-temporal region with rTMS. These effects are suggested to result from a facilitated access to perceptual information provided by the right hemisphere, with decreased competition from linguistic and semantic processes usually carried in the affected left-temporal regions (Miller et al., 2000; Miller et al., 1998; Snyder, 2003). Indeed, in a further experiment Chi et al. (2010) report a notorious improvement in a visual memory task by inhibition of the anterior left temporal lobe and simultaneous stimulation of the homolog right side through transcranial direct current stimulation (tDCS).

Overall, the previous examples support how on different domains, competition between the hemispheres through inhibition is an important factor that affects the quality of task processing, and that these "opponent processes" (Kapur, 1996) affect the final behavioral output.

1.3 BRAIN LATERALITY AND SKILLED VISUOMOTOR PERFORMANCE

A balanced interaction between the hemispheres is essential for skilled visuomotor performance, as different phases of the task demand for different brain resources (Beckmann et al, 2013). Skilled performance in golf putting, archery, and gun shooting has been widely studied with EEG (Hatfield et al., 2004) and fMRI (Milton et al., 2004), observing a pattern of lateralized activations that are modulated according to the level of expertise of the subject, and the stage of performance. During the initial learning of the task, there is increased activation of left prefrontal and temporal regions including language centers, reflecting the need for executive control and reliance on self-talk (Lacourse, et al. 2005; Deeny et al., 2003; Doyon & Ungerleider, 2002; Springer & Deutsch, 1998). Once expertise is acquired, executive regulation decreases and prefrontal activation resides (Hatfield, et al. 2004), shifting predominant activity to those sites most directly relevant to the task at hand: e.g. in shooting and archery, the right parietal cortex for visual processing is prominent (Milton et al., 2004; van Mier et al., 1998; Salazar et al., 1990); in golf putting and karate wood-breaking, heightened activity is observed over sensorimotor areas (Crews & Landers, 1993; Collins, 1990). In this way, visual and motor areas become dominant without competitive interference from executive processes from the prefrontal cortex and linguistic processes of the left-temporal cortex (Beckmann et al., 2013; Hatfield et al., 2004). Indeed, EEG studies show that the level of reduction of activity in the anterior left-hemisphere region during performance correlates positively with the level of expertise between subjects (Deeny et al., 2003; Haufler, et al. 2000), and the accuracy of performance within subjects (Kerick, *et al.,* 2004). Conversely higher left hemispheric activation in skilled individuals is associated with a decrease in their otherwise high performance (Salazar, 1990).

This sequence of activations during the learning process is in accordance with the classical model of motor-skilled acquisition by Fitts and Posner (1967), and like the model, reflects a process in which the learner at first makes great cognitive effort to control movement, but as performance improves the execution is relegated to passive control mechanisms and the task becomes automatized (Hatfield et al., 2004; Milton et al., 2004; Haufler, 2000). It can be said that reduction of nonessential cortical features, is indispensable for this automatization in skilled visuo-motor performance, reducing competitive interference (Hatfield et al., 2004; Haufler, 2000). Indeed in expert performers, a state of generalized attenuation of cortical arousal, as reflected by an increase in EEG alpha power, has been observed just before task-specific activations take place in rifle shooting (Haufler et al, 2000) and Karate wood-breaking (Collins et al., 1990). Alpha power increases are indicative of a decrease in cortical activity (Sauseng et al., 2009; Romei et al., 2008; Klimesch et al. 2006). It is suggested that this generalized reduction is a requisite for the following task-specific activations to take place, since it first shouts down unspecific activity, and reduces competitive interference (Hatfield et al., 2004; Haufler et al, 2000; Collins et al., 1990).

1.4 VISUOMOTOR SKILL FAILURE UNDER PRESSURE AND ITS PROPOSED BRAIN MECHANISM

Although over the course of learning the execution of motor skills becomes more effortless and automatic, well-learned skills sometimes break down, particularly under conditions of pressure to perform well, producing visuomotor-skill failure (Beckmann et al. 2013; Baumeister, 1984). Such pressure conditions can be either competition, presence of an audience, reward or punishment contingencies, or ego relevance (Baumeister & Showers, 1986). Self-monitoring is a possible account for motor-skill failure, that is, when pressure leads the performer to increase conscious attention to the process of action, so that each step of the execution sequence is consciously monitored and the automatic nature of skilled-performance is disrupted (Baumeister, 1984; Beilock and Carr, 2001). Support for this proposal comes from studies in which visuomotor skill failure under pressure did not occur because self-monitoring was inhibited by directing attention to a secondary task (Beilock & Carr, 2001), or because the participants learned the task implicitly without declarative knowledge (Masters, 1992). Moreover, Hossner and Ehrlenspiel (2010) observed that when proficient basketball players were asked to consciously monitor various verbally marked parts of a free throw, they produced over-proportional muscular activation that disrupted the natural execution of the movement, in contrast to when they were simply instructed to shoot; analogous findings have been observed for golf putting (Gucciardi & Dimmock, 2008). Within the Fitts and Posner model (1967), this self-monitoring implies a regression from the autonomous performing phase, to the initial cognitive phase (Beckmann et al., 2013).

In terms of cortical activity, self-monitoring induced by pressure to perform may disrupt the balanced interaction between the hemispheres necessary for skilled performance (Beckmann et al. 2013), so that competition from left anterior areas disrupt the necessary right parietal activations. One study supports this notion. Linder et al. (1998) analyzed the EEG alpha band during a golf putting task under pressure and observed that those participants who showed motor-skill failure had a dominant left-sided activation, while those who did not worsen their performance had a more balanced activation between the two hemispheres. Because of the lateralization of language and executive processes to the left hemisphere, this result supports the proposition that pressure induces self-monitoring, and implies that it produces a regression from the dominant right-sided activity of visual and motor areas prominent in skilled performers, to the left-sided areas characteristic of the initial learning phase. Lee and Grafton (2015) used a special version of the game "snake" as a visuomotor task under pressure for performance-contingent monetary rewards in the fMRI. When analyzing activity before each trial, they report increased bilateral activation of the dorsolateral prefrontal cortex (DLPFC), and increased connectivity with the motor cortex prior to movement onset, which correlated with skill failure trials (albeit the intensity of that activation correlated with a lesser propensity to fail). However, not only the DLPFC showed greater activation in skill failure trials, but also the striatum, likely reflecting modulations of arousal (Lee & Grafon, 2015; Mobbs et al., 2009; Chib et al., 2012), and anterior cingulate cortex (ACC) probably reflecting conflict detection (Lee & Grafton, 2015). These activations could be said to reflect the components that constitute the concern for performance, which leads towards self-monitoring as seen in cortical activity patterns in EEG.

In summary, according to Beckmann et al. (2013) it can be said that pressure engenders the desire to perform well, so that attention is directed inward in order to consciously monitor the execution of motor action. But this creates a disadvantageous hemispheric asymmetry in which the left hemisphere brings competitive interference that obstructs the dominance of the right parietal regions necessary for skilled visuomotor action, and performance is disrupted. Although other brain regions appear to be involved in the process of skill failure, it is the disruptions over the cortex which ultimately account for the final motor output in the task.

1.5 DYNAMIC HANDGRIP AND THE PREVENTION OF VISUOMOTOR-SKILL FAILURE

Considering that left-hemispheric dominance just before skilled-motor performance represents a competitive interference with the required right hemisphere, Beckmann et al. (2013) aimed to prevent this dominance from taking place, hence prevent skill failure from occurring. For this purpose, they used unilateral handgrip exercises. Handgrip exercises have been shown to induce greater relative activity of the contralateral over the ipsilateral hemisphere, making it dominant (Harmon Jones, 2006; Peterson et al. 2008; see following paragraphs). Beckmann et al. (2013) used an intermittent grip, or "dynamic handgrip" (Kluess, 2000; Napadow, 2008) which consisted of vigorously pressing a rubber ball for 30 seconds before performing: with the left hand for the experimental groups, to induce right hemisphere dominance, or with the right hand for the control groups to induce left hemisphere dominance. In the experiment, the performance of experienced athletes was tested under pressure induced through competition, a large audience, and performance evaluation in three sports: football penalty shots, tae-kwon-do kick combination, and badminton service. Performance of each group was compared between a pressure free baseline without ball pressing, and under pressure after ball pressing.

In all three sports, participants who pressed the ball with the left hand (right hemispheric dominance) were resistant to motor-skill failure, while those who used the right hand (left hemispheric dominance) were not. Notably, the badminton service study included two measurements under pressure, one with dynamic handgrip and one without it. In the left-grip group, performance declined under pressure during the no handgrip block respective to baseline, but it recovered once the dynamic handgrip was introduced. Meanwhile in the right-grip group, performance continued to decline under pressure even after handgrip was introduced.

As a slight form of exercise, handgrip manipulations have been long used to investigate the reaction of the body to physical exercise, and are known to affect multiple systems of the body. The form of the handgrip can be either “static” by keeping the hand contracted for a period of time (e.g. Sander et al., 2010; Millar et al., 2009), or “dynamic”, by continuously alternating between contraction and distention during an interval (e.g. Kluess et al., 2000; Napadow et al., 2008). The contractions can be done through pure fist clenching (e.g. Meleis et al., 1982), grip devices (e.g. Kluess et al., 2000), or rubber balls (e.g. Harmon Jones, 2006). Among the reactive systems are mainly the circulatory (Kluess et al., 2000; Napadow et al., 2008; Ray & Carrasco, 2000; Brook et al., 2013), but also autonomic nervous system (Kluess et al., 2000; Millar et al., 2009; Napadow et al., 2008), cortical (Meleis et al., 1982; Liu et al., 2003; Sander et al., 2010) and sub-cortical systems (Napadow et al, 2008; Sander et al., 2010). However, long-term effects after execution have also been observed. For example, acute systolic hypotension following a single handgrip bout in healthy population, likely owing to para-sympathetic modulations (Millar et al., 2009-2), as well as reductions of resting systolic blood-pressure in hypertensive patients who regularly execute handgrip routines (Brook et al., 2013; Millar et al., 2009) and in healthy population with those same routines (Ray & Carrasco, 2000; Millar et al., 2009-2).

In the psychological domain, handgrip exercises are reported to modify behavior in tasks introduced subsequently (e.g. Beckmann et al., 2013; Propper et al., 2013; Goldstein et al., 2010; Harmon-Jones, 2006; Schiff et al., 1998). Since these psychological effects necessarily have a biological substrate, the aforementioned physiological aftereffects could logically account for this altered behavior, for example greater para-sympathetic (Millar et al., 2009-2) and less sympathetic (Sinoway et al., 1996) activity after handgrip. However, a particularity of handgrip research in psychology, is that its aftereffects have been dependent on whether the right or the left hand were used, implying differences in the physiological effects produced by each hand. Early on in the field, it was reasoned that unilateral contractions could leave a lasting effect on the contralateral hemisphere to the active hand through spreading activation from the motor cortex, rendering that hemisphere with greater activity levels relative to the other (Schiff & Lamon, 1994; Schiff et al., 1998). Though these differences must necessarily be very slight (Davidson et al., 1988; Peterson et al., 2008). The nature of the behavioral aftereffects has been used to support the former argument (Schiff et al., 1998; Goldstein et al., 2010; Propper et al., 2013; Gable et al., 2013). For example, based on the robust findings which associate the frontal right hemisphere with negative emotions, and the left hemisphere with positive emotions (Davidson, 2004), some studies report inducing a propensity towards positive emotional states after right contractions (enhancing the left hemisphere), and towards negative ones after left contractions (enhancing the right hemisphere) (Schiff & Lamon, 1994). Although the participants did not report outwardly feeling such emotional states, they were reflected in subsequent tasks such as judging the emotion of neutral faces (Schiff & Truchon, 1993), or in the content of stories that participants created when shown pictures of the TAT projective test (Schiff & Lamon, 1994).

Similar to Beckmann et al. (2013) in sports, other authors have used handgrip in the laboratory to enhance performance on tasks supported to rely strongly on the hemisphere contralateral to the hand used for contractions. Goldstein et al., (2010) report enhanced performance in the Remote Associates Test, a measure of creative thinking through word associations, after left, but not after right hand contractions (Goldstein et al., 2010). According to Goldstein et al., since evidence supports that the Remote Associates Test strongly depends on the right hemisphere (Jung-Beeman et al., 2004), shifting hemispheric dominance to the right through left handgrip improved performance in the task. Propper et al. (2013) observed enhancements of memory encoding after right, and retrieval after left contractions, but not the opposite. The hypothesis was based on the hemispheric Encoding/Retrieval Asymmetry (HERA; Tulving et al., 1994) model of memory, which proposes that left prefrontal regions are associated with memory encoding, while right prefrontal regions, with retrieval. In the domain of perception, Gable et al., (2013) report enhanced reaction times to global stimuli after left contractions, and to local stimuli after right contractions in the global-local letter task (Fig 1.1). Gable et al., (2013) also assessed the N1 event-related potential (ERP) during task performance after handgrip, and report a marginally significant N1 amplitude increase towards local targets after right contractions, suggesting slightly enhanced processing of these stimuli. Since the right-parietal hemisphere is associated with the processing of global features of visual stimuli, and the left-parietal hemisphere with local features (Gazzaniga, 2000; McGilchrist, 2010; Boksem et al., 2012), Gable et al. (2013) lend support to the hemispheric dominance induction hypothesis.

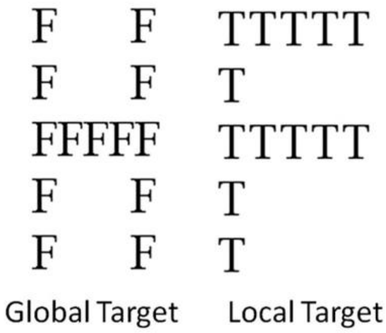

Fig 1.1: Example of the Navon Global-Local letter stimuli. The task consists in indicating as quickly as possible whether the picture contains a target letter. In this example, the global target is the letter *H*, made of smaller *F*s; the local target is the letter *T*, which composes a larger *F*. Adapted from Gable et al. (2013) with permission.

Three EEG studies have compared the effects of left and right static handgrip on hemispheric activity levels during grip execution. In each of these studies participants vigorously pressed a rubber ball in a static fashion. Two groups are contrasted, each executing handgrip with either right or left prior to performing a task where the behavioral effects of the handgrip were expected. An activation asymmetry index is derived from the alpha band levels for each group (Davidson, 2004) and differences between the groups' indices are tested. In this way, Harmon-Jones (2006) reports that dynamic handgrip produces effects over large contralateral areas. As expectable, electrodes over the contralateral motor regions showed greater activity than ipsilateral ones during handgrip, but most importantly, this same pattern of activity was also observed for frontal, temporal and parietal electrode locations. In subsequent studies, Peterson et al. (2008) and Gable et al., (2013) report similar findings. Behaviorally, Harmon Jones (2006) reports more positive evaluations of a neutral broadcast if participants performed right handgrip while listening. Peterson et al (2008) report more aggressive behavior in a competitive game after right handgrip. Gable et al. (2013) report the aforementioned enhancement of global attention after left, and local attention after right handgrip. These EEG studies then support the idea that broad cortical areas co-activate with the contralateral motor network of the same hemisphere during contractions, inducing a greater activation levels of that hemisphere and making it dominant over the other.

1.5.1 Limitations of EEG-Handgrip research in psychology

From the aforementioned EEG studies, a remarkable limitation is that the permanence of the allegedly induced activation asymmetry has not been directly assessed once handgrip is terminated, but is rather assumed based on the behavioral outputs. Furthermore, at least two behavioral studies (see next section) using the handgrip manipulation report either contradictory results (Turner et al., 2016), or no effects (Nicholls et al., 2001).

Hence, it is possible that mechanisms other than an induced hemispheric activation asymmetry take place after handgrip exercise, which require being examined on their own right. For instance, bilateral activations during high force and long lasting movements such as handgrip exercise are well known (Nirkko, et al., 2001; Liu et al, 2003; Hamzei et al., 2002; Yang et al., 2011). It is then conceivable that aftereffects on cortical activity following handgrip could affect both hemispheres. From the aforementioned EEG studies, only Harmon-Jones (2006) reports the activation levels between the hemispheres within subjects, showing bilateral activation, but greater activation levels on the contralateral hemisphere. In contrast, Peterson et al. (2008) removed 12 out of 36 participants from analysis, who did not show asymmetry effects during handgrip, while Gable et al., (2013) only report the asymmetry index between hemispheres. This conflictive evidence requires further analysis.

1.5.2 Conflicting findings

Despite reported evidence supporting the induction of hemispheric dominance through handgrip, there are conflicting behavioral and neuro-physiological findings. For instance, Turner et al. (2016) obtained the opposite results of Goldstein et al. (2010) in the Remote Associates Test, so that participants who performed right static handgrip, and not left handgrip, showed greater creativity in the test. By itself, this finding contradicts either the notion that the right hemisphere is more involved in creative thinking than the left, or the notion that handgrip biases hemispheric asymmetry. A further study supports the latter case. Nicholls et al (2001) observed no effect of dynamic handgrip on the gray-scales task, a measure of attentional asymmetry (Nicholls et al., 2004). Since attentional asymmetry reflects hemispheric activation asymmetry (Kapur et al., 1996; Vuilleumier et al., 1996; Hilgetag, et al., 2001; Oliveri et al. 2001), this lack of effects implies that dynamic handgrip did not increase the relative activation of one hemisphere over the other.

From a physiological perspective, although it is known that single movements produce contralateral excitation and ipsilateral inhibition of the primary motor cortex (Allison et al., 2000; Hamzei et al., 2002), this is truth presumably only within a short window of about 100 ms (Liepert et al., 2001); and finer fMRI methods have revealed that even within this time window an ipsilateral activation of pre-motor areas occurs (Nirkko et al., 2001). On the other hand, with tonic contractions such as static handgrip, or otherwise high force levels as in dynamic handgrip, a net ipsilateral excitation is observed (Wassermann et al., 1994; Liepert et al., 2001; Liu et al, 2003; Yang et al., 2011). Wasserman et al., (1994) were able to induce motor evoked potentials (MEP) of the hand ipsilateral to TMS brain stimulation but only if the participants facilitated the induction by keeping a constant ipsilateral abduction of the index finger, implying an ipsilateral increase of cortical activity. Tinazzi and Zanette (1998) also found increased ipsilateral excitability during contralateral movement. Liepert et al. (2001) compared the ipsilateral motor response to TMS during single phasic and sustained contralateral pinch-grips, and noted that while phasic pinch-grips decreased ipsilateral MEPs, sustained pinch-grips increased them. Sustained pinch-grips are analogous to static handgrip, and cortical excitability towards TMS reflects the state of cortical activation (Sauseng et al., 2009; Romei et al., 2008; Klimesch et al. 2006), therefore these results suggest that static handgrip, in contrast to single short lasting movements, produces a net excitation of the ipsilateral motor cortex. This has been further clarified in EEG and fMRI studies.

Yang et al. (2011) followed the time course of activity over the cortex produced by submaximal right hand contractions held for three seconds. Source analysis of EEG signals showed a bilateral linear signal increase of the sensorimotor cortex, which started 1000 ms before movement (reflecting motor preparation), peaked at force onset, declined 100 ms after force onset, and rose again after 500 ms. As expectable, the contralateral signal was predominant at movement preparation and onset, however the overall activation profile between the hemispheres equalized at the later stages of sustained effort (Fig 1.2, Fig 1.3). The left pre-motor and supplementary motor areas showed the same pattern of activation, but their right counterparts were not included in the analysis. In an fMRI experiment, Liu et al. (2003) compared the effects of exhaustion caused by submaximal right-static and dynamic handgrip sustained for prolonged times (between 4 to 15 min). The exerted force over a handgrip device remained stable for static handgrip, and declined slightly for dynamic handgrip. Despite relatively stable force levels, electromyographic signals showed a steady increase along both contraction periods, suggesting a gradual recruitment of more motor units in order to keep the same force level. Likewise, for both types of handgrip, the fMRI signal showed at first a steep increase of the contralateral primary sensorimotor cortex, which then turned to a steady increase up to a plateau. Most importantly for the current topic, also the ipsilateral primary sensorimotor cortex, and the bilateral prefrontal cortex, supplementary motor area, cingulate gyrus, and cerebellum showed steady increases along both static and dynamic handgrip.

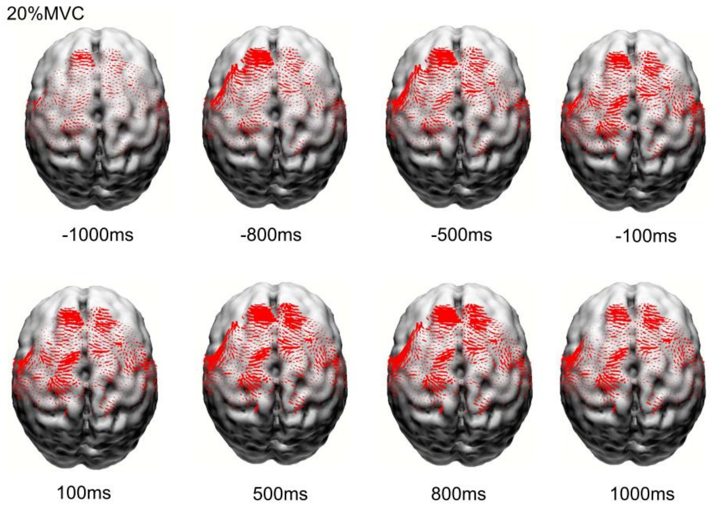

Fig 1.2: Reconstructed normalized and averaged cortical currents at 20% maximal voluntary contraction force of 8 subjects at eight time points from early preparation to holding phases of the handgrip task. The size of the red dots is proportional to the local current density. Only currents in motor related cortical area (left M1, left S1, PM & SMA, right M1 and S1) are shown here. The current density exhibited non-linear alterations throughout the motor process. Adapted from Yang et al. (2011) with permission.

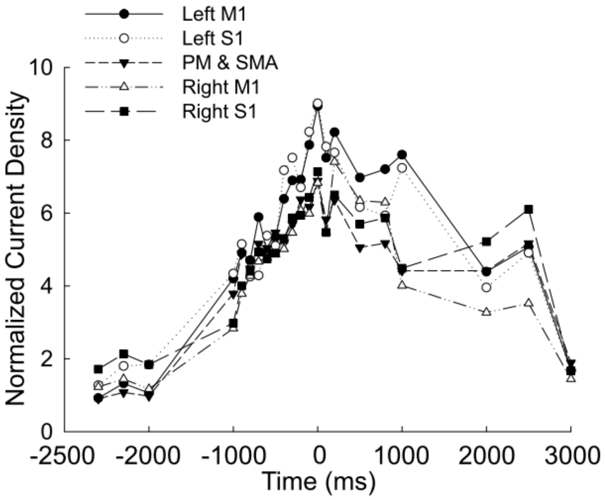

Fig 1.3: Averaged and normalized current density plotted as a function of time in the motor related cortical area (left M1, Left S1, PM & SMA, right M1, right S1) in 8 subjects at 20% maximal voluntary handgrip force. Time '0' is the force onset. Negative time values indicate time points before force onset. Adapted from Yang et al. (2011) with permission.

The former experiments which specifically examined the handgrip exercise, show that both, its static and dynamic variants produce a bilateral activation of sensorimotor areas, accompanied by co-activation of frontal and sub-cortical areas, and the activation profile tended to assimilate between the two hemispheres after a few seconds of continuous effort. Similar phenomena is observed with other kinds of movements. Deiber et al. (2001) found no significant difference between the activation levels of the hemispheres during unimanual finger sequences, as reflected by the EEG alpha band. Dettmers et al. (1996) found an increase of ipsilateral activity during dynamic key pressing, as reflected by positron emission tomography (PET). A decline in ipsilateral activity was observed only for the lowest force levels (5% of maximal voluntary contraction; MVC). In the same study, ipsilateral reactivity to TMS pulses also increased during static key pressing at high force levels (40% and 60% MVC), indicating an increase of cortical activity. For the handgrip contractions in psychological experiments the participants are always asked to press a rubber ball completely with all fingers (eg. Harmon Jones 2006; Beckmann et al., 2013), which involves high levels of force, therefore, most likely producing bilateral activations, although this pattern has only been explicitly reported by Harmon-Jones (2006).

1.5.3 Possible alternate aftereffects handgrip

So far it is apparent with diverse measuring techniques, that different kinds of unimanual movements like finger extensions, pinch grips or finger sequences produce similar cortical activation patterns than dynamic and static handgrip. Hence these studies can cue towards the missing information in handgrip experiments, namely, the differences between left and right unimanual movements, and the state of the cortex after their execution. Deiber et al. (2001) compared cortical activation during left, right and bimanual finger sequences in right handers. Apart from finding bilateral widespread activations for left, right and bimanual sequences, the left (non-dominant) and bimanual finger sequences produced greater activation than right sequences (Fig 1.4, Fig 1.5). Key pressing frequency was constant for all conditions, so that it did not play a role in activation intensity. With different bilateral activation intensities for the left and right hand, it could be possible that the same kind of aftereffect, but with different intensity, remains on both cortical hemispheres after unimanual movements, such as handgrip exercise.

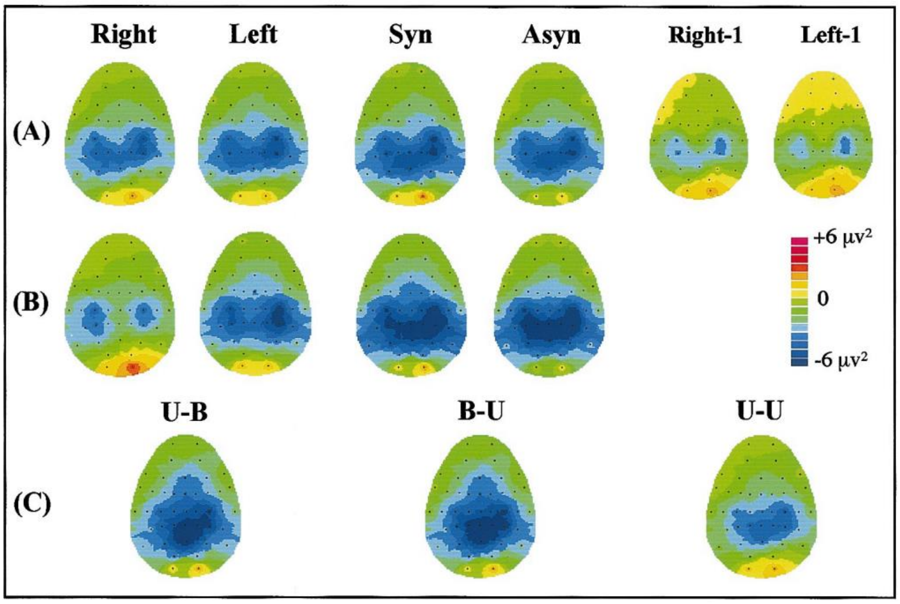

Fig 1.4 Grand averaged of topographic task-related power maps (*n* = 10) in the lower alpha band (7.8-9.8 Hz). The dots indicate electrode positions. Task-related power decreases (area of 'activation', negative power values) are coded in blue/green and task related power increases (positive power values) are coded in red/orange. (A) Initiation of motor sequences, corresponding to epoch 1 of right, left, bimanual synchronous or asynchronous. Right-1 and Left-1 correspond to a condition of transition from left to right and right to left unimanual sequences respectively. (B) Steady state execution of motor sequences. Maps corresponding to steady state execution of unimanual sequences for Right-1 and Left-1 are similar to the maps illustrated in row B for Right and Left, respectively, and are not illustrated for simplification. (C) Transition between unimanual and bimanual, and bimanual synchronous to asynchronous motor sequences. Note the bilateral distribution of task related power decrease at initiation and stable execution of the sequences, contrasting with the mesioparietal distribution at transition between motor sequences. Adapted from Deiber et al. (2001) with permission.

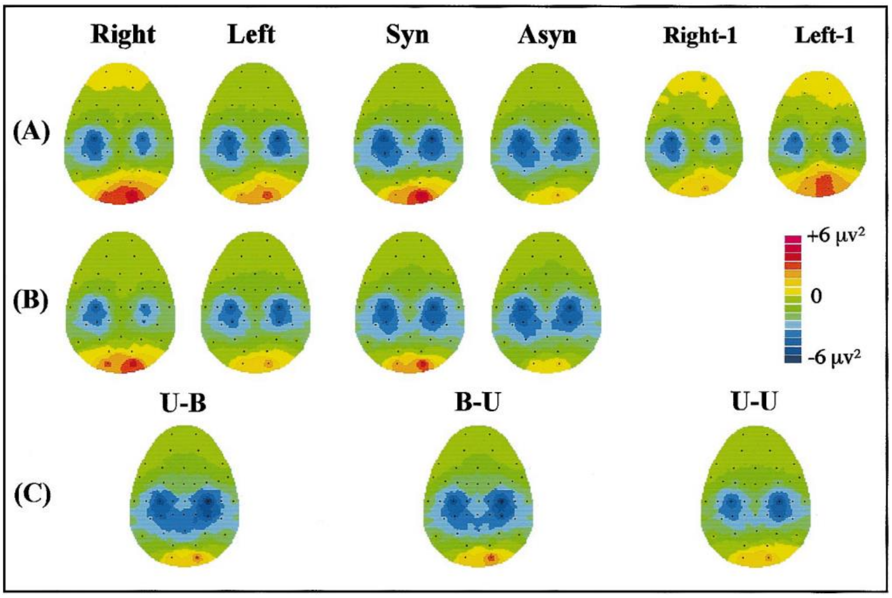

Fig 1.5. Grand average of topographic task=related power maps (*n* = 10) in the upper alpha band (10.8-11.8 Hz). Same conventions as in Fig 1.4. Adapted from Deiber et al. (2001) with permission.

The cortical aftereffects of continuous hand movements have been little studied. Some TMS studies give a cue of the state of the cortex after unimanual exercise. Zanette et al. (1995) observed a reduction of motor-evoked response of the right hand for 35 min after one min of repetitive abduction of the right thumb. McKay et al. (1995) found the same result after tonic contraction of the tibialis anterior muscle of the right leg, with aftereffects lasting for 20 min. Bäumer et al. (2002) observed reduced responsivity to TMS in both hands, up to 15 minutes after executing fatiguing pinch grips with the left hand. Bonato et al. (1996) found a MEP reduction on the left thenar eminence (TE) after exercise of the right, but this reduction appeared 10 min post-exercise (Fig 1.6). In all experiments, no change was found in indicators of passive nerve conductance, supporting that the observed effects are of brain origin. The time courses and location of the effects in these studies reveal a complex dynamics in the cortex after exercise. Nonetheless, the effect observed by Bäumer et al. (2002) over both hands, induced by exercise of the left hand, suggests a differential effect where left hand movements may produce a greater attenuation of brain activity than right hand movements. The results of Bonato et al. (1996) for exercise of the right hand are similar, but are not immediate, appearing 10 min post exercise. EEG is a suitable tool to analyze the immediate aftereffects following exercise of each hand, on both hemispheres and extended regions of the scalp. In the current case, the exercise of interest is dynamic handgrip as used by Beckmann et al. (2013).

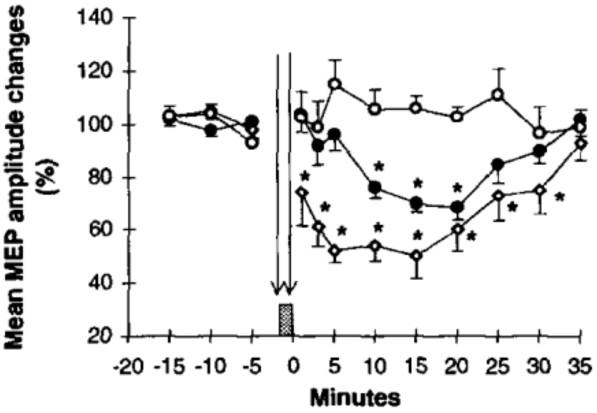

Fig 1.6: Mean and SE of MEP amplitude changes to TMS relative to the left (•) and right (◊) TE muscles and the left biceps branchialis (○) at different stimulation times before and after 1 min exercise of the right thumb. Exercise started at min-1 and lasted 1 min. The grey bar and arrows indicate the duration of exercise. Post-exercise MEPs were recorded at min 1, 3, 5 and then at 5 min intervals up to 35 min. Each value is the average of MEP percentage differences compared to a baseline value taken as 100%, obtained from the mean of three pre-exercise trials. *Significantly different from pre-exercise values. Significance was found for the left TE muscles at post-exercise min 10-20 and for the right TE at post-exercise min 1-30 (Wilcoxon $P < 0.01$). Adapted from Bonato et al. (1996) with permission.

1.6 RATIONALE BEHIND THE CURRENT STUDIES

Psychological EEG experiments with handgrip manipulations suggest the induction of one sided hemispheric dominance after contractions as a basis for behavioral aftereffects. However this proposal is only assumed based on the behavioral aftereffects themselves, and on observations during contractions using between-subjects designs. Given the usual interest in testing behavioral after effects, this proposal has not been directly assessed. In the current work, the physiological and behavioral effects of handgrip were tested in two separate EEG experiments.

The first aim was to clarify the cortical aftereffects that take place following dynamic handgrip as used by Beckmann et al. (2013) on their experiment to prevent visuo-motor skill failure in sports. Specifically it was tested whether dynamic handgrip would induce a state of biased contralateral activity after termination, as assumed in psychological handgrip experiments; or if it produced a reduction of cortical activity after conclusion, as suggested by TMS experiments which used similar static and dynamic exercises, and to what intensity with each hand. The latter hypothesis is based upon the literature which shows that dynamic and static exercises similar to handgrip also generate comparable activation patterns. Likewise, the literature shows similar activation patterns for dynamic handgrip as used by Beckmann et al. (2013) and static handgrip as used by Harmon-Jones (2006), Peterson et al. (2008) and Gable et al. (2013). In this way, the mechanism behind behavioral aftereffects of handgrip reported in psychological experiments could be further clarified. The EEG measurements used were alpha amplitude, and alpha asymmetry ratio.

The following aim, was to replicate the prevention of visuo-motor skill failure under pressure through left-dynamic handgrip as in the experiment by Beckmann et al. (2013), while also assessing task-related EEG modulations. For that purpose, an EEG-suitable task that assimilated the fluid nature of sportive tasks used by Beckmann et al. was necessary. A special version of the video game “Pong” was customized for the study. In previous studies using Pong, task related EEG-modulations have been already identified, similar to those reported in sports experiments. In that way, good performance in Pong is correlated with greater right than left central-parietal activation (Rebert & Low, 1978), or in other words dominance of right central-parietal regions while performing. Rebert et al. (1984) further identified fronto-central enhancements of the EEG theta band, but did not explore correlations with performance. Based on the current literature, it was expected that performance in Pong under pressure would alter such EEG modulations, and dynamic handgrip with the left hand would attenuate this effect. The EEG measurements used were alpha asymmetry ratio and theta amplitude. As in previous experiments (Rebert & Low, 1978; Rebert et al. 1984), eye movements were greatly reduced by having a play screen of 7° visual angle, and were further corrected pre-analysis. A ball swing of around 1 Hz further prevented eye movements to contaminate the EEG ranges of interest.

1.7 EEG MEASUREMENTS

1.7.1 EEG alpha band and alpha asymmetry

The EEG alpha band is inversely correlated with the level of cortical activity (Klimesch et al. 2006). Hence it is also inversely correlated with reactivity to TMS stimulation (Sauseng et al., 2009; Romei et al., 2008), and TMS studies of the cortical state after dynamic and static exercise report a reduction of reactivity. Finally, alpha is also the most common measure in EEG studies of skilled performance (Hatfield et al., 2004). Dynamic handgrip could produce a general attenuation of cortical activity as in TMS studies but reflected as an increase of alpha amplitude in EEG. This alpha amplitude increase would also mimic the increase observed just before task-specific activations take place in experienced athletes (Cheron et al., 2016; Haufler et al., 2000; Collins et al., 1990). This activity attenuation (increased alpha amplitude), induced through dynamic handgrip would then facilitate the subsequent activation of right hemispheric regions necessary in visuomotor performance, without competitive interference from the left (Janelle & Hatfield, 2008 Hatfield et al., 2004; Haufler et al, 2000; Collins et al., 1990). It has been further observed that moderate increases in alpha amplitude imply a state of readiness for processing information, higher levels of alpha before task or trial engagement correlate with better performance (Doppelmayr et al., 1998; Klimesch, 1999; Klimesch et al., 2006; Jensen & Mazaheri., 2010; Hatfield et al., 2004).

Alternatively, the contralateral dominance observed by Harmon Jones (2006) and Peterson et al. (2008) during the handgrip, could persist for a long time after the end of the handgrip. This would imply a direct induction of the right hemisphere dominance necessary for visuomotor performance, if the dynamic handgrip is done with the left hand. For the current purposes, this activation dominance can be explored through asymmetries in alpha levels, just as done in the studies of Harmon Jones and Peterson et al. but including a post-handgrip measure. Alpha asymmetry reveals differences in the activation levels between two homologue areas of the hemispheres, which are observable upon task engagement as well as during rest (Davidson, 1988). Though very small, these activation differences at rest are known to influence different behavioral traits depending on which cortical regions they are located on, such as mood tendencies for the frontal lobes (Davidson, 2004), or level of skill for visual-spatial perception seen for the parietal lobes (Davidson, 1988). When performing in Pong, greater right parietal activity is expected (rightward asymmetry), which might be disrupted by pressure induction. Inducing a resting rightward asymmetry in advance would then facilitate task-related activations to take place.

1.7.2 EEG theta band

Rebert et al. (1984) noted an enhancement of frontal-central theta while playing “Pong” as an unexpected finding when they revisited data from an older study (Rebert & Low, 1978). They proposed that EEG theta activity is involved in aspects of attentional or motor control in the task, but did not explore its correlations with performance. The theta band has been consistently seen in relation to tasks with higher cognitive demand or need for conscious control (Cavanagh & Frank, 2014; Sauseng et al., 2007). It is also used as a marker of “cognitive workload” in studies of driver performance in automobiles or operation of machinery (Brouwer et al., 2012). In a driving video game, theta levels were modulated by the introduction of a secondary task with varying degrees of difficulty (Anguera et al., 2013), but not by the game itself. In such context, it calls attention that an enhancement of theta amplitudes was observed in a fluid visuomotor task like “Pong”. Based on the Fitts and Posner (1967) model for motor acquisition, in the current work it is hypothesized that theta amplitudes in Pong might reflect proficiency levels in the game, so that greater amplitudes imply greater cognitive control and less automatization of the task, hence lesser proficiency. Therefore, if visuomotor skill failure implies a regression from automatic to supervised performance on a task, as proposed by Beckmann et al (2013), this would be reflected in higher theta levels, and left-dynamic handgrip could prevent it from happening.

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Chapter 2

Aftereffects of dynamic handgrip[1]

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RESEARCH ARTICLE

Unilateral Left-Hand Contractions Produce Widespread Depression of Cortical Activity after Their Execution

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Abstract

The execution of unilateral hand contractions before performance has been reported to produce behavioral aftereffects in various tasks. These effects have been regularly attributed to an induced shift in activation asymmetry to the contralateral hemisphere produced by the contractions. An alternative explanation proposes a generalized state of reduced bilateral cortical activity following unilateral hand contractions. The current experiment contrasted the above explanation models and tested the state of cortical activity after the termination of unilateral hand contractions. Twenty right-handed participants performed hand contractions in two blocks, one for each hand. Using electroencephalogram (EEG), the broad alpha band and its asymmetry between hemispheres before, during, and after hand contractions were analyzed. During contractions, significant bilateral decrease in alpha amplitudes (indicating cortical activation) emerged for both hands around sensory-motor regions. After contractions, alpha amplitudes increased significantly over the whole scalp when compared to baseline, but only for the left hand. No modulation of hemispheric asymmetry was observed at any phase. The results suggest that unilateral hand contractions produce a state of reduced cortical activity after their termination, which is more pronounced if the left hand was used. Consequently, we propose that the reduced cortical activity (and not the persistent activation asymmetry) may facilitate engagement in subsequent behavior, probably due to preventing interference from other, nonessential cortical regions.

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Data Availability Statement: All Alpha Amplitude Measurements—Linked Mastoids files are available from the FigShare database (figshare.com/s/09f3fc60134711e5910206ec4bbcf141). All Alpha Amplitude Measurements—Average Reference files are available from the FigShare database (http://figshare.com/s/f4f2443a8c7111e5bcec06ec4bbcf141). All Alpha Amplitude Measurements—Surface Laplacian files are available from the FigShare database (http://figshare.com/s/16ff5a9a8c7211e5b71a06ec4bbcf141). All Upper Alpha/Mu Rebound Measurements are available from

Introduction

The present research tested the changes in the state of cortical activity after the termination of unilateral hand contractions. Unilateral hand contractions, also referred as hand clenching, consist of executing a vigorous grip movement with one hand for a brief period of time (e.g., [1–7]). Numerous studies [1–7] report that unilateral hand contractions produce particular behavioral effects after their execution. These effects have been attributed to an induced shift in activation asymmetry to the contralateral hemisphere induced through the contractions, hence

the FigShare database (http://figshare.com/s/0f05af9c8c7211e5b7c906ec4bbcf141). All Broad Alpha Rebound Measurements are available from the FigShare database (http://figshare.com/s/091049a88c7211e5b7c906ec4bbcf141). All Beta (22 Hz) Rebound Measurements are available from the FigShare database (http://figshare.com/s/01f55b188c7211e58d2706ec4bbcf141).

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enhancing the functions in which that hemisphere specializes and affecting performance in a subsequent task. Among the reported effects are heightened approach motivation after right contractions [1, 2, 4]; increased processing to global visual stimuli after left, and local stimuli after right contractions [5]; enhanced memory encoding after right, and retrieval after left contractions [3]; and prevention of motor skill failure under pressure after left hand contractions [6]. In the above studies, it is assumed that the activation asymmetry towards the contralateral hemisphere induced through unilateral hand contractions persists even after their termination (referred to hereafter as a *persistent activity model*). However, this notion has not been tested directly and an alternative mechanism is possible.

The persistent activity model suggests that during the hand contractions, activity spreads from the contralateral motor cortex towards adjacent regions in the same hemisphere, producing a one sided increase in basal hemispheric activity which persists after terminating contractions and thus affects subsequent behavior [4, 6, 7]. Electroencephalogram (EEG) studies found a greater relative left activation during the right hand contractions and a greater relative right activation during the left hand contractions [1, 2, 5]. Moreover, this biased activation asymmetry towards the contralateral hemisphere affected not only the motor area, but was also observed over frontal, temporal and parietal locations, supporting the notion that during contractions, activity of the motor cortex recruits other adjacent cortical regions. This overspread activity might thus facilitate subsequent behaviors that rely on the functions of the involved hemisphere [8].

An alternative explanation, referred to hereafter as a *reduced activity model*, can be deduced from experimental findings using Transcranial Magnetic Stimulation (TMS). A long-lasting depression of cortical excitability has been reported after the execution of repetitive unilateral hand movements similar to the hand contractions [9–11]. When using the right hand (lifting a weight with the wrist [9]; abduction-adduction of the thumb [10]), the depression has been observed at the contralateral hemisphere; when using the left hand (pinch grips, [11]) the depression has been observed at both hemispheres. This suggests that while activity is increased in the contralateral hemisphere *during* unilateral hand contractions [1, 2, 5], a state of reduced cortical activity may take place *after* the contractions, which is probably more widespread if the left hand was used [9–11]. Empirical evidence further supports that a tonic reduction in cortical activity, reflected by an increase in the EEG alpha band, implies a state of readiness for processing information [12–15], and preparing motor actions [16–19]. Consequently, the reduced cortical activity might contribute to enhanced cognitive and motor performance by facilitating task-specific cortical activations, and preventing interference from other, nonessential cortical regions [13–17, 20, 21].

Thus, these two explanatory models make different predictions about how unilateral hand contractions affect cortical activity and subsequent task performance. The persistent activity model predicts that the induced dominant activation of the contralateral hemisphere observed during unilateral hand contractions [1, 2, 5] prevails after their termination. The reduced activity model predicts that after the termination of unilateral hand contractions, a generalized state of reduced cortical activity emerges. In addition, based on current findings [9–11], we assume that the left and right hands might differ regarding the strength of the effect. These predictions were tested in the present EEG experiment. In particular, we analyzed the amplitude of the EEG broad alpha band (8–12 Hz) and its asymmetry between hemispheres before, during and after hand contractions. Alpha band power represents the inverse of cortical activation [13, 14, 22] and is known to affect the cortical response to TMS [23–28], therefore reflecting a state similar to that observed in TMS experiments after repetitive hand movements.

Distinguishing between the two hypothesized effects of unilateral contraction is relevant for a better understanding of the mechanisms underlying the reported behavioral aftereffects of hand contractions. Furthermore, if hand contractions induce an increase of alpha amplitudes after their termination, they may represent an additional alternative to other established methods of alpha entrainment like repetitive TMS (rTMS) [29] or transcranial alternating current stimulation (tACS) [22, 30] with their prospective clinical applications.

Materials and Methods

Study Design

The study used a within-subjects design in which the effects during and after contractions of each hand on cortical activity were analyzed in comparison to their respective baselines through EEG. Differences between baselines were also analyzed. Only data of right handed subjects were included. In order to examine only the effects produced by unilateral hand contractions on cortical activity, no further tasks were tested. To prevent the experiment from getting too long, hence to avoid possible confounds of tiredness or boredom on the EEG, only one single series of repetitive hand contractions was carried for each hand. Note that in a previous study by our research group a single series of contractions sufficed for producing subsequent behavioral effects [6].

Participants

Twenty five voluntary participants were recruited for the experiment. Three of the participants were not included for analysis due to technical errors. One participant was left handed as indicated by the Edinburgh Handedness Inventory [31] and therefore, her data were removed. Another participant had to abandon the experiment owing to breathing problems due to a spring allergy. The final sample consisted of 20 right-handed participants (11 female), with a mean age of 22.9 years (range: 19 to 26 years). Their mean laterality quotient was +82.23 (range: +52.94 to +100). Prior to entering the study, all participants were informed of the procedures, assured the right to quit the experiment at any moment with no consequences, and asked to sign an informed consent according to the Declaration of Helsinki. The study did not concern medical research neither involved any invasive or potentially dangerous methods for participants and, in accordance with the German Science Foundation, formal approval was not required. At the Technishe Universität München, behavioral sciences are a relatively new area and an ethics committee is in process of being established. At present, projects are presented in a colloquium in which ethical considerations are also discussed. The current research has found approval in such a colloquium.

Task and Apparatus

Participants sat comfortably on a padded chair in a silent, ample room with attenuated light. The hand contraction task consisted in holding a soft rubber ball (6 cm diameter) in one hand and squeezing it completely with all fingers at a self-pace towards an approximate rate of two times a second, for 45 seconds, while keeping the other hand over their lap with the palm facing down. A small camera outside participants' view allowed the experimenter to verify correct task performance. To reduce eye movements, participants were requested to look at a grey fixation cross against a black background, presented on a computer screen. To facilitate fixation, the cross flickered from gray to white for 10 msec at variable intervals of 2, 4 or 6 seconds. The same flicker was used for all experimental conditions.

Procedure

Participants were informed that the experiment tests brain activity patterns elicited by hand movements. After signing an informed consent, participants completed the Edinburgh

Handedness Inventory [31]. The scale consists of 10 items where participants rate their preference regarding hand use in various activities such as writing, drawing, throwing, or using scissors. Laterality coefficients range from -100 to +100, and a person is considered to be right-handed when his or her value is higher than +50. Before EEG preparation, participants were instructed how to execute the hand contractions, given an example, and were requested to demonstrate correct understanding. The procedure was shown by the experimenter once again before starting the recording. EEG recording was carried out in two blocks, one for each hand (hand-blocks). Each hand-block consisted of three phases: a two minute resting baseline, 45 seconds of hand contractions and two minutes resting after contractions. After completing one hand-block, a two minute break followed in which the participant could stretch, in order to prevent carry over effects before the next measurement. Before resuming recording, electrode impedances were checked again. Next, a new block was recorded for the other hand. The initial hand-block was counter-balanced. In order to reduce effects of preparation of movement over brain activity, during all resting recordings, the rubber ball stayed at reach behind the participants, outside visual range. For every baseline, the participants were informed in advance which hand was going to follow.

EEG recording and pre-processing

EEG was recorded with a 64 Ag/AgCl active electrode actiCAP system (Brain Products, Munich, Germany), over an elastic cap (Easy Cap, FMS), with electrodes placed according to the international 10/10 system [32]. All electrodes were referenced to position FCz, and afterwards offline re-referenced to linked mastoids (TP9, TP10). The ground electrode was placed at location AFz. Vertical electrooculogram (VEOG) was registered from an electrode placed beneath the left eye and Fp1. Data was recorded with a Brain Amp amplifier (Brain Products, Munich, Germany), using a band-pass filter from 0.1 to 250 Hz and a notch filter set at 50 Hz, with a sampling rate of 1000 Hz. All electrode impedances were kept under 3 kΩ to prevent large impedance differences between homologous sites. Before EEG analysis, all data was visually inspected to remove large artifacts, re-sampled to a power of two (1024 Hz) and filtered using an infinite-impulse-response (IIR) filter as implemented in Brain Vision Analizer 2 [33] with a high pass of 0.5 Hz, a low pass of 40 Hz and 24 dB slope, notch filter enabled at 50 Hz. An infomax independent component analysis (ICA) as implemented in Brain Vision Analyzer 2 [34, 35] was run and high energy components that reflected eye movements were subtracted.

Continuous EEG recordings were segmented into 2 sec contiguous epochs with 50% overlap for the phases before, during and after contractions of each hand. Automatic artifact rejection was performed on each epoch with a maximum allowed amplitude of ±100 μV, maximum allowed voltage steps of 50 μV between two sampling points, and a minimum required signal change of 0.5 μV in 500 ms. Spectral amplitudes were extracted through a fast Fourier transformation using a Hamming Window with a 50% overlap between contiguous epochs, leading to a spectral resolution of 0.5 Hz. All the 2 sec artifact free epochs within each phase were averaged together. Based on Harmon Jones [1] and Peterson et al. [2], we extracted amplitudes of the whole range of the broad alpha band (8–12 Hz) for homologous electrode pairs Fp1-Fp2, F3-F4, F7-F8, C3-C4, FC3-FC4, FT7-FT8, CP3-CP4, T7-T8, P7-P8, P3-P4, O1-O2 of the 10/10 system, and analyzed the obtained amplitudes and their asymmetry ratio ([right-left/right+-left]; [36]).

Data Analyses

Alpha amplitudes of single electrodes were submitted to a repeated measures ANOVA with the factors "electrode" (Fp1, Fp2, F3, F4, F7, F8, C3, C4, FC3, FC4, FT7, FT8, CP3, CP4, T7, T8, P7, P8, P3, P4, O1, O2), "hand-block" (left, right), and "phase" (before, during and after contractions).

Likewise, the obtained asymmetry-ratios from paired homologue electrodes were submitted to a repeated measures ANOVA with the factors "pair" (Fp1-Fp2, F3-F4, F7-F8, C3-C4, FC3-FC4, FT7-FT8, CP3-CP4, T7-T8, P7-P8, P3-P4, O1-O2), "hand-block" (left, right) and "phase" (before, during and after contractions). Greenhouse-Geisser values are reported when necessary. All significant results from the analyses were post-hoc analyzed with pairwise *t*-tests, using Bonferroni adjusted alpha levels, and their effect sizes assessed with Cohen's d_z [37]. To confirm analyses, all EEG data was further re-processed with an Average-Reference, and with a reference-free surface-Laplacian [38–42], and the statistical procedures were repeated. For all analyses, an interaction of the factors "hand-block" and "phase" would indicate that hand contractions modulated the alpha amplitudes or asymmetry ratios across the measuring phases.

To gain further insight, we also explored the cortical reaction immediately following hand contractions. Planned comparisons based on previous literature [43–46] were implemented using the broad (8–12 Hz) and upper (10–12 Hz) alpha bands. In these comparisons, the grand-average amplitudes at the first second of the post-contraction period, were compared with the last second of the contraction period [44, 45], and with the last three seconds post-contractions. Fourier transforms over epochs of one single second led to a spectral resolution of 1 Hz. In order to explore the spread of these effects over the scalp, we analyzed electrodes C3, C4, O1, O2 [44, 47], as well as frontal locations F3 and F4 [25, 40, 41, 48].

Results

Alpha amplitudes

The repeated measures ANOVA revealed a significant main effect of phase, $F(2, 38) = 20.36$, $p = .001$, $\eta_p^2 = .52$. Post-hoc t-tests corrected for 3 comparisons, with all scalp electrodes averaged for each phase with both hands, indicated that regardless of the hand-block, greater alpha amplitudes were observed before contractions ($M = 1.91$, $SD = .60$) than during contractions ($M = 1.76$, $SD = .54$), $t(19) = 2.94$, $p = .02$, $d_z = .74$, and weaker than after contractions ($M = 2.07$, $SD = .70$), $t(19) = -4.10$, $p = .002$, $d_z = .92$. Consequently, weaker alpha amplitudes were observed during contractions than after contractions, $t(19) = -5.67$, $p = .001$, $d_z = 1.27$. The analysis further revealed a significant main effect of electrode, $F(21, 399) = 22.67$, $p = .001$, $\eta_p^2 = .58$, which merely implies amplitude differences among various electrodes to others throughout the whole experiment. There was no main effect of hand-block, indicating that the average alpha amplitudes of the two hand-blocks across all recording phases did not differ significantly.

Our main interest was in how cortical activity changes during and after contractions as a function of the hand used. The analysis revealed a significant interaction of phase and hand-block, $F(2, 38) = 3.47$, $p = .04$, $\eta_p^2 = .15$, which indicates that amplitude changes within each electrode at each phase were modulated by the hand used for contractions. Table 1 shows alpha amplitudes for all analyzed single electrodes during the two hand-blocks. Post-hoc *t*-tests comparing the values within each electrode across phases for each hand separately are summarized in Table 2. During contractions, significant bilateral decreases in alpha amplitudes took place for both hands around sensory-motor regions, followed by a marked increase after contractions which, compared to baseline, was statistically significant only for the left hand at all electrode locations except F8 and O1. Fig 1 plots alpha amplitudes in every electrode for each hand-block at all phases. Accompanying difference maps display the subtraction of alpha

Table 1.

Electrode Position	Left Hand Contractions			Right Hand Contractions		
	Before	During	After	Before	During	After
Fp1	1.61 (.48)	1.46 (.46)	1.82 (.65)	1.75 (.59)	1.59 (.51)	1.79 (.61)
Fp2	1.59 (.47)	1.45 (.40)	1.78 (.62)	1.72 (.54)	1.56 (.47)	1.73 (.56)
F3	1.76 (.59)	1.61 (.52)	1.99 (.74)	1.86 (.67)	1.71 (.61)	1.92 (.70)
F4	1.78 (.55)	1.64 (.47)	1.99 (.71)	1.91 (.64)	1.75 (.57)	1.94 (.66)
F7	1.66 (.54)	1.55 (.48)	1.91 (.76)	1.77 (.65)	1.65 (.62)	1.85 (.67)
F8	1.66 (.50)	1.53 (.43)	1.83 (.67)	1.75 (.60)	1.63 (.56)	1.79 (.60)
C3	1.90 (.61)	1.65 (.43)	2.14 (.77)	1.99 (.66)	1.69 (.50)	2.05 (.70)
C4	1.94 (.64)	1.71 (.48)	2.19 (.75)	2.06 (.66)	1.76 (.54)	2.13 (.69)
FC3	1.78 (.57)	1.61 (.46)	2.02 (.73)	1.89 (.62)	1.68 (.55)	1.93 (.65)
FC4	1.81 (.54)	1.69 (.47)	2.03 (.68)	1.92 (.60)	1.73 (.52)	1.94 (.59)
FT7	1.61 (.57)	1.49(.45)	1.86(.73)	1.68(.63)	1.57(.58)	1.80(.63)
FT8	1.54 (.54)	1.47 (.42)	1.74 (.66)	1.62 (.60)	1.52 (.57)	1.67 (.63)
CP3	2.06 (.65)	1.76 (.44)	2.31 (.82)	2.13 (.66)	1.79 (.49)	2.20 (.70)
CP4	2.11 (.75)	1.81 (.52)	2.36 (.85)	2.21 (.71)	1.92 (.60)	2.33 (.80)
T7	1.45 (.59)	1.34 (.47)	1.71 (.75)	1.56 (.55)	1.44 (.50)	1.69 (.65)
T8	1.41 (.62)	1.37 (.50)	1.67 (.77)	1.50 (.65)	1.40 (.60)	1.65 (.70)
P7	2.08 (.73)	1.88 (.63)	2.33 (.94)	2.16 (.75)	1.95 (.69)	2.28 (.83)
P8	2.05 (.73)	1.93 (.73)	2.36 (.91)	2.18 (.74)	2.07 (.82)	2.35 (.85)
P3	2.21 (.74)	1.99 (.62)	2.48 (.94)	2.31 (.75)	2.04 (.61)	2.40 (.81)
P4	2.19 (.74)	2.02 (.69)	2.48 (.90)	2.30 (.72)	2.16 (.75)	2.43 (.81)
O1	2.35 (.78)	2.38 (1.02)	2.65 (1.10)	2.49 (.96)	2.47 (1.07)	2.61 (1.00)
O2	2.31 (.81)	2.34 (1.02)	2.64 (1.10)	2.46 (.93)	2.49 (1.08)	2.60 (1.02)

Mean (*SD*) alpha amplitudes for each electrode and each hand across the phases.

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amplitudes of the baselines from their respective periods during and after contractions of each hand. Bilateral decreases in alpha can be observed during contractions for both hands, while after contractions, a generalized increase in alpha amplitude is evident only for the left hand. The right hand shows a smaller and more focal alpha-increase which only reached statistical significance at electrodes P8 and O2.

A comparison of the baselines before left and right contractions revealed significant differences at frontal electrodes (S1 Table), with higher alpha amplitudes before right hand contractions. A closer inspection revealed that in those participants which first performed the left hand-block, the increase in alpha amplitudes prevailed through the baseline before right-contractions (S1 Fig). Therefore, to certify that the observed increase of alpha amplitudes only after left contractions was not confounded by the order of the hand-blocks, a complementary analysis was implemented. The sample was split into right-first and left-first sub-groups, and *t*-tests comparing alpha values before and after contractions were repeated for each sub-group. Given the smaller size of the sub-groups, Bonferroni correction was not considered. This analysis confirmed that in each sub-group, while the left hand produced significant increases in alpha amplitudes after contractions at most electrodes (S2 Table), the right hand produced smaller increases in fewer electrodes. In sum, these results support the reduced activity model. Cortical activity declined after the termination of hand contractions, this effect was however more pronounced for the left hand.

Table 2.

Electrode Position	Left Hand Contractions				Right Hand Contractions			
	Before vs. During		Before vs. After		Before vs. During		Before vs. After	
	t(19)	d_z	*t*(19)	d_z	*t*(19)	d_z	*t*(19)	d_z
Fp1	2.71*	.61	-3.53**	.79	2.19	.49	-1.23	.28
Fp2	2.45	.55	-3.31**	.74	2.44	.55	-2.82	.63
F3	2.67*	.60	-3.97**	.89	2.38	.53	-1.72	.38
F4	2.27	.51	-3.56**	.80	2.58	.58	-1.11	.25
F7	2.16	.48	-3.26*	.73	1.66	.37	-2.15	.48
F8	1.76	.39	-2.53	.57	1.55	.35	-1.11	.25
C3	3.98**	.89	-3.30*	.74	3.76**	.84	-.91	.20
C4	3.45**	.77	-4.37**	.98	3.87**	.87	-1.38	.31
FC3	2.83*	.63	-3.51**	.79	3.37*	.75	-.87	.19
FC4	1.93	.43	-3.83**	.86	3.13*	.70	-.52	.12
FT7	2.07	.46	-3.70**	.83	1.75	.39	-2.02	.45
FT8	1.13	.25	-3.82**	.85	1.37	.31	-.998	.22
CP3	4.52**	1.01	-3.64**	.81	4.17**	.93	-.909	.20
CP4	3.86**	.86	-4.65**	1.04	4.55**	1.02	-2.23	.50
T7	1.94	.43	-3.38**	.76	1.92	.43	-1.68	.38
T8	.64	.14	-3.60**	.81	1.34	.30	-2.45	.55
P7	2.55	.57	-3.26**	.73	3.07	.69	-2.14	.48
P8	1.01	.23	-3.59**	.80	1.39	.31	-3.74**	.84
P3	2.83*	.63	-3.76**	.84	3.88**	.87	-1.30	.29
P4	1.81	.40	-4.38**	.98	2.14	.48	-2.58	.58
O1	-.023	.01	-2.73	.61	.186	.04	-2.55	.57
O2	-.024	.01	-3.52**	.79	-.338	.08	-3.12*	.70

t-scores and effect sizes for differences in alpha amplitudes between the phases before and during and the phases before and after hand contractions for each electrode and each hand.

*indicates significance $p < .016$, and

**indicates significance $p < .003$ (corrected for multiple (3) comparisons–Bonferroni).

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A further interaction was observed between electrode and phase, $F(42, 798) = 4.49$, $p = .002$, $\eta_p^2 = .19$, indicating that amplitude differences among electrodes varied with each phase. Post-hoc analysis displayed in the supplementary material (S1 Annex, S2 Fig) revealed that occipital and central electrodes increased the difference between their amplitudes during hand contractions of any hand. This owes to the fact that during contractions, occipital electrodes slightly, albeit non-significantly, increased their alpha amplitudes (Table 1), while central electrodes showed the greatest decrease. This observation is in line with classical findings in the literature where hand movements produced a simultaneous activation on motor regions over the scalp, and inhibition over visual regions [47].

No interaction of electrode and hand-block was observed, indicating that the differences between electrodes were not affected by the hand used. Finally, the three-way interaction of hand-block, electrode and phase was not significant. In the confirmation analysis with alternative EEG referencing schemes (S2 Annex) the Surface Laplacian corroborated the currently observed effects, namely, an interaction between phase and hand-block $F(2, 38) = 3.29$,

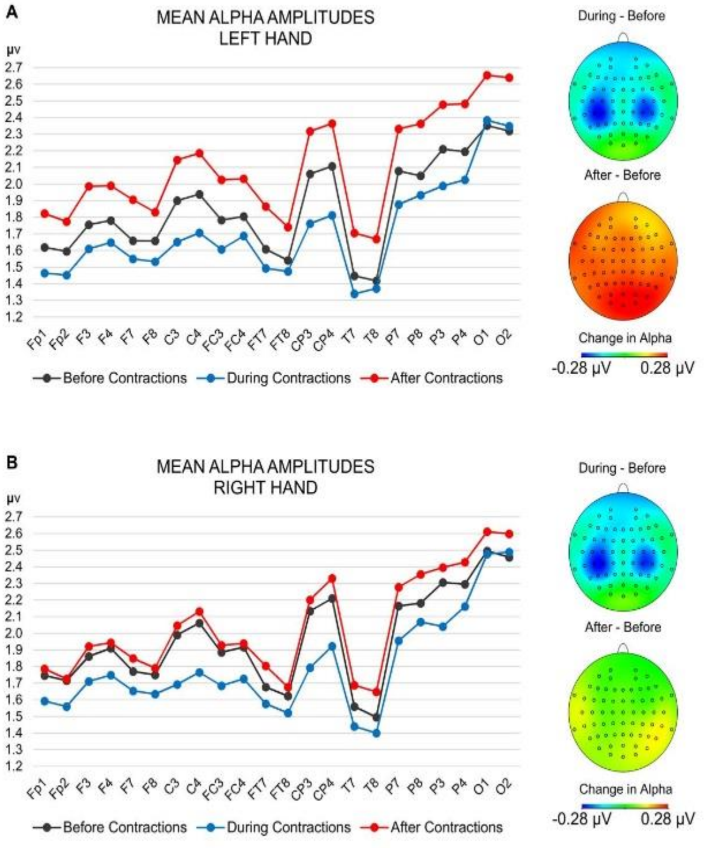

Fig 1. Plot of the alpha amplitudes at each electrode before, during and after contractions. A) For the left hand-block. B) For the right hand-block. Accompanying difference maps indicate the distribution of amplitude changes on the scalp when subtracting the baseline before contractions from the phases during and after contractions.

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$p = .048$, $\eta_p^2 = .15$, while the average reference showed the same patterns, albeit the aforementioned interaction did not reach statistical significance $F(2, 38) = 2.43$, $p = .101$, $\eta_p^2 = .11$.

Alpha asymmetry ratios

Tests for asymmetry ratios showed any main effects neither of hand-block, pair, phase or their interactions. The lack of interaction between the factors phase and hand-block, $F(2, 38) = .43$, $p = .65$ $\eta_p^2 = .02$, indicates that hand contractions did not induce systematic modulations of asymmetry within each electrode pair. This lack of effect can be visualized in Fig 1, where despite of overall amplitude changes at each phase, the amplitude ratio between homologue electrodes (i.e., F3-F4, C3-C4, etc.) remains mostly constant and is not systematically modified by left or right hand contractions. Thus, we could not replicate the findings of Harmon-Jones [1] and Peterson et al. [2] who reported greater relative activation in electrodes contralateral to the active hand. Consequently, our results are contrary to the persistent activity model.

Cortical reaction immediately following contractions

Explorative comparisons based on previous literature [43–46] revealed a bilateral amplitude increase restricted to the upper alpha range (10–12 Hz) over motor regions immediately following left hand and to a lesser degree, right hand contractions (Fig 2). In the first second after left contractions this increment was significant on electrodes C3 ($M = 4.18$ µV, $SD = 2.39$) and

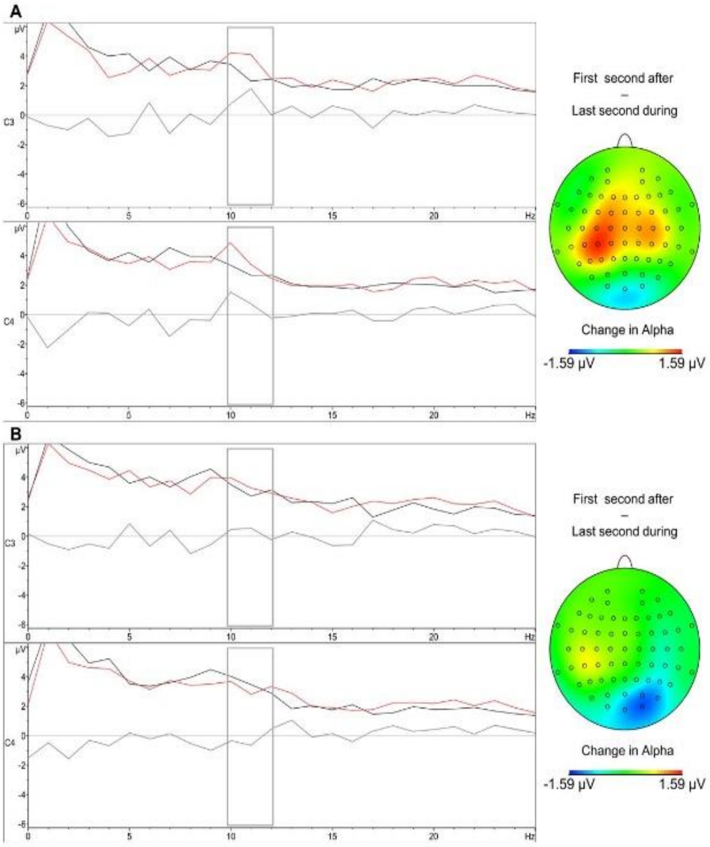

Fig 2. Spectral plot of the last second during contractions (black), first second after contractions (red), and their difference (gray). A) For the left hand-block. B) For the right hand-block. The gray rectangle highlights the upper alpha band. Accompanying difference maps illustrate the difference over the scalp when subtracting the last second of contractions, from the first second after contractions.

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C4 ($M = 4.14$ µV, $SD = 1.85$) compared with their respective last second during contractions in C3 ($M = 2.89$ µV, $SD = 1.23$) $t(19) = 2.48$, $p < .05$, $d_z = .55$ and C4 ($M = 3.01$ µV, $SD = 1.21$), $t(19) = 3.03$, $p < .01$, $d_z = .68$. An accompanying peak was observed at 22 Hz over C3 (Fig 2) after termination ($M = 2.71$ µV, $SD = 1.35$) over the last contraction second ($M = 2.01$ µV, $SD = 1.17$) with marginal significance $t(19) = 1.98$, $p = .06$, $d_z = .44$, which likely represents a harmonic component of the upper alpha enhancement [44]. These observations coincide with previously reported rebounds of the Mu rhythm, an inhibitory rhythm of the motor cortex which overlaps with the upper range of alpha [44, 48] after single hand movements [44, 46].

When comparing upper alpha at C3 and C4 in the first second after left contractions with the last three seconds of the same period, no significant differences were found. This is given that the already enhanced upper alpha at the first second covers part of the broad alpha band (8–12 Hz), which also showed enhancements in the last seconds (Fig 3). Therefore, if the former comparison is carried using broad alpha, the antepenultimate and penultimate seconds show a significant amplitude increase, although the last second fails to reach significance (Table 3).

With the right hand, a contralateral rebound of upper alpha was observed at C3 (Fig 3), but did not reach statistical significance, no ipsilateral rebound at C4 was observed (Fig 3). This suggests that although a unilateral rebound of the Mu rhythm was observable after right contractions as in previous reports [43; 44], it had lesser intensity, and could not exceed the statistical threshold on the present setting (only one trial per participant). When comparing upper

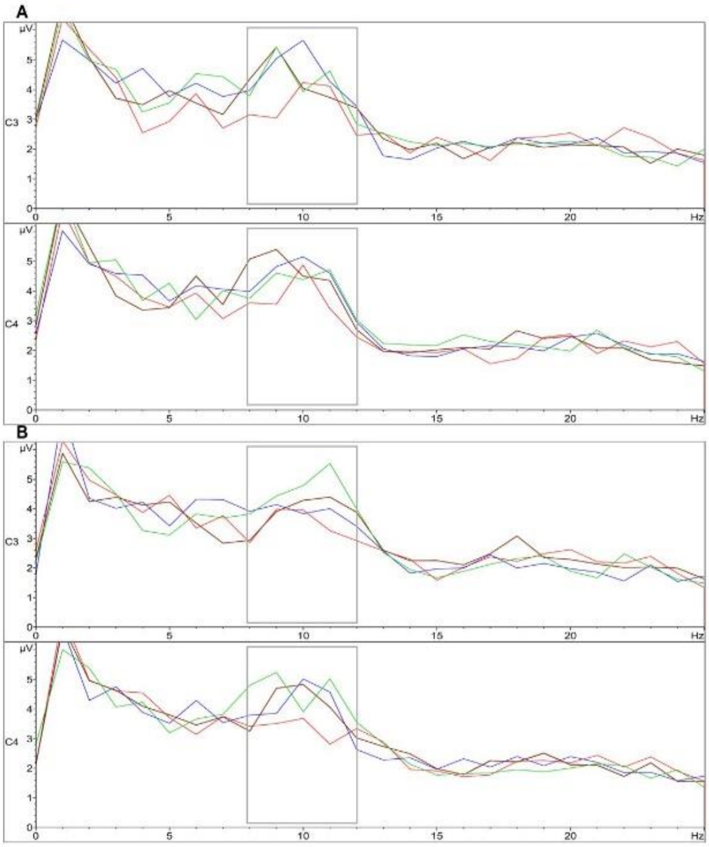

Fig 3. Spectral plot of the first (red), antepenultimate (blue), penultimate (brown) and last (green) seconds after contractions. A) For the left hand-block. B) For the right hand-block. The gray rectangle highlights the broad alpha band.

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alpha in the first second after contractions at C3 ($M = 3.61$ μV, $SD = 2.10$) and C4 ($M = 3.25$ μV, $SD = 1.46$) versus the respective last three seconds, a significant enhancement is observed in the last second at C3 ($M = 5.16$ μV, $SD = 2.87$), $t(19) = -2.53$, $p < .05$, $d_z = .57$ and C4 ($M = 4.47$ μV, $SD = 2.43$), $t(19) = -2.10$, $p = .05$, $d_z = .47$, owing to increases in the broader alpha band at the end (Fig 3). Therefore, when using broad alpha for the same comparison, a significant increase is observed for the last second for both at C3 and C4 (Table 3), and at the antepenultimate second over C4 only (Table 3).

Frontal and occipital electrodes included in this analysis did not show significant changes in upper or broad alpha immediately following hand contractions. However, when comparing the first second versus the last three seconds after contractions, most electrodes showed increases in broad alpha with the left, and less consistently with the right hand (Table 3). On Table 3, although statistical significance is not always reached, most likely due to the current blocked experimental-design having a simple sample per participant, the mean amplitudes, *t*-values and their respective effect sizes tend to be greater for the left hand, except for the last second.

Overall, these observations suggest that immediately after contractions, an inhibitory reaction was triggered initially at the motor cortex, with greater intensity after left contractions, as indicated by increases in upper alpha/Mu amplitudes. Subsequently, this inhibition covered broader areas as shown by increases in the broad alpha amplitude in occipital, motor and frontal electrodes in the last three seconds. This inhibition was more consistent after left than after right contractions.

Table 3.

Broad alpha amplitude after contractions: Left hand										
	Firstsecond	AntepenultimateSecond			PenultimateSecond			Lastsecond		
	Mean	**Mean**	***t*(19)**	**d_z**	**Mean**	***t*(19)**	**d_z**	**Mean**	***t*(19)**	**d_z**
C3	3.64	4.74	-3.15**	.70	4.39	-2.44*	.55	4.44	-1.62	.36
C4	3.86	4.64	-2.18*	.49	4.83	-2.77*	.62	4.36	-1.15	.26
F3	3.40	4.18	-1.57	.35	3.92	-1.42	.32	4.30	-1.87	.42
F4	3.28	4.41	-3.01**	.67	4.01	-1.99	.44	4.33	-2.11*	.47
O1	3.95	6.21	-3.99**	.89	6.12	-3.31**	.74	5.25	-2.62*	.59
O2	4.24	5.54	-3.10**	.69	6.53	-3.34**	.75	5.52	-2.01	.45
Broad alpha amplitude after contractions: Right hand										
	Firstsecond	AntepenultimateSecond			Penultimatesecond			LastSecond		
	Mean	**Mean**	***t*(19)**	**d_z**	**Mean**	***t*(19)**	**d_z**	**Mean**	***t*(19)**	**d_z**
C3	3.52	3.98	-1.16	.26	3.88	-1.04	.23	4.65	-2.71*	.61
C4	3.36	4.31	-2.10*	.47	4.21	-1.58	.35	4.75	-3.04*	.68
F3	3.59	3.60	-.01	0	3.69	-.27	.06	4.50	-2.50*	.56
F4	3.56	3.63	-.25	.06	3.80	-.66	.15	4.44	-2.17*	.49
O1	4.21	5.57	-2.39*	.53	5.47	-2.80*	.63	5.75	-2.92**	.65
O2	4.25	5.48	-2.90**	.65	6.02	-4.42**	.99	5.32	-2.17*	.49

t-scores and effect sizes for differences in alpha amplitudes between the first second after contractions and the last three seconds of the same period.
*indicates significance $p < .05$, and
**indicates significance $p < .01$.

doi:10.1371/journal.pone.0145867.t003

Discussion

Numerous studies report that unilateral hand contractions produce particular behavioral effects after their termination [1–7], but the underlying mechanism is still not clear. One group of researchers [e.g., 4, 6, 7] proposed that unilateral hand contractions induce a shift in activation asymmetry to the contralateral brain hemisphere, which persists even after the termination of hand contractions. An alternative explanation, which comes from TMS research [9–11], states that a generalized state of reduced cortical activity emerges after the termination of unilateral hand contractions. The aim of the present experiment was to shed more light onto this issue by testing cortical activity during and after hand contractions. In particular, using the EEG alpha band, we contrasted if the hemispheric activation during contractions would prevail after their termination (the persistent activity model), or if a reduction of cortical activity would emerge (the reduced activity model). Our results favor the reduced activity model. Whereas a bilateral activation over motor areas was observed during contractions with any hand, we found a long lasting reduction of cortical activity below baseline over the whole scalp after contractions, which was especially evident when the left hand was contracted. These results suggest that the behavioral aftereffects induced through unilateral hand contractions are mediated by reduced cortical activity.

To the best of our knowledge, we are the first who compared the effects of unilateral hand contractions *after* their termination with a baseline before contractions using EEG. Increases in the alpha range, which reflect decreased cortical activity, have been related to reductions of the cortical response to TMS pulses [23–28]. Therefore, the currently observed increase of alpha after hand contractions (especially of the left hand) is similar to previous observations with TMS [e.g. 9, 10, 11]. Zanette et al. [10] observed a response reduction on the right hand for 35 minutes after one minute of repetitive abduction of the right thumb. Bäumer et al. [11]

observed reduced cortical response to TMS for both hands, up to 15 minutes after executing pinch grips with only the left hand.

The reduction of cortical activity after hand contractions may be explained by inhibitory mechanisms. According to TMS scholars e.g., [10, 49], inhibitory mechanisms are massively activated after repetitive hand movements in order to control for neuronal hyper-excitability, and they are gradually turned off during a recovery period of several minutes. In our data, the onset of these inhibitory mechanisms was reflected by an enhancement in the upper alpha range over motor electrodes (known as "Mu rhythm" [43, 44; 48]) in the first second after the end of contractions, coinciding also with previous event-related studies of single hand movements [43, 44]. This rebound was bilateral after left hand contractions, and was greater than that after right contractions, which was only contralateral and did not reach statistical significance. The last three seconds of the period after contractions, showed enhancements of the broad alpha band that cover the initial upper alpha rebound, and mimic the broad alpha increase seen for the average of the whole two minute period. Moreover, the last three seconds also showed alpha enhancements in occipital and frontal areas, similar to the whole-scalp alpha enhancement seen for the two-minute average, which suggests inhibitory action also at these locations.

While TMS studies can prove a long lasting depression of cortical excitability over the involved sensory-motor cortex and its homologue contralateral region after repetitive movements, our current alpha band measurement revealed this reduction of activity also in regions away from sensory-motor areas. Distant regions uniformly decreased their activation levels for a long period after contractions. This might be accounted for by the complex interactions that occur over the cortex during hand movements. Inhibition of occipital areas during single hand movements has previously been reported [47]. In this experiment, occipital electrodes were the only ones to increase, albeit slightly, their alpha amplitudes during contractions. As already shown, this inhibition carried on and intensified towards the post-contractions period. On the other side, frontal areas are involved in the control of hand movements [43, 50, 51] and, like motor areas, need to be down-regulated after movement implementation [43, 51]. During contractions, we observed significant anterior activations at FC3, FC4, Fp1, and F3, which became subsequently inhibited along the period after contractions. In a study with epileptic patients, Derambure et al [51] observed that patients with focal motor seizures, as well as those with temporal lobe epilepsy took considerably longer to deactivate sensory-motor and frontal regions after single hand movements compared to healthy participants, further supporting the importance of these inhibitory mechanisms in healthy brains.

We assume that during contractions, the activation of the network involved in motor action further influenced other cortical regions through complex axonal pathways [52, 53], but local inhibitory mechanisms prevented their over-excitation [10, 41, 49, 52, 54]. Inhibitory mechanisms acting at separate locations from active cortex have been proposed [41, 52]. Although these inhibitory mechanisms become most evident in studies of epilepsy, they are presumably analogous to those present in healthy population [41, 52, 54–56]. In epileptic patients, the fact that pathological activity can quickly spread to distant, even multi-lobar regions supports that long axonal pathways can transfer activity beyond the trigger area [52, 53]. Furthermore, when seizures fail to spread, activity at surrounding and distant regions is still influenced by the ictal focus, before it normalizes through the intervention of local inhibitory mechanisms [52]. In support of the former arguments, it has been reported that clenching the fist can produce generalized spike-wave discharges in epileptic patients [57]. The aforementioned inhibitory restrain has also been observed *in vitro* [52, 55, 56] and is presumed to be the analogous to the surround inhibition seen during normal motor performance [41, 47, 58]. In our sample with healthy population, we propose that this traveling activity from the motor network is balanced out by local inhibitory mechanisms without reaching pathological levels. As mentioned by Trevelyan et al. [55], the same inhibitory mechanisms may restrain less intense forms of activity.

Altogether, we propose that the observed increment in alpha amplitudes after contractions results from inhibitory mechanisms that first activate during contractions to control cortical excitability [10, 41, 49], prevent the spread of activity [10, 41, 49, 52, 54], and provide movement specificity [47, 58]. The long lasting alpha increase parallels the recovery period seen in TMS experiments [9–11], and may then reflect a longer lasting action of the inhibitory mechanisms after hand contractions are finished, as proposed by Zanette et al. [10] and Bonato et al. [49]. Notably, the strength of cortical inhibition after unilateral hand contractions was observed at all regions after left-hand contractions while for the right hand, this effect was much weaker, and seldom reached statistical significance. We propose this may result from the greater level of white matter and connectivity of the right hemisphere (which mostly commands the left hand) towards the rest of the brain [59–63], prompting inhibitory mechanisms to a greater extent.

Cortical activity *during* hand contractions also deserves mention. Contrary to the persistent activity model, we found no effect over hemispheric activation asymmetries during hand contractions (neither after contractions). Thus, our results are at odds with previous EEG studies [1, 2, 5]. This might be due to differences in experimental design. The previous experiments had been between-subjects, whereas we used a within-subject design. Similar studies with within-subjects designs also observed bilateral sensorimotor activations during unilateral hand contractions. For example, using functional magnetic resonance imaging (fMRI), Liu et al. [64] observed steady increase of fMRI signal in both contralateral and ipsilateral hemispheres during hand contractions. This observation also coincides with other EEG studies which used different kinds of repetitive unilateral movements like finger taping [65] or rhythmic flexion movements of the index finger [50]. Using positron emission tomography (PET) and TMS, Dettmers et al. [66] observed an increase in regional blood flow and of cortical excitability (both implying cortical activation) of both motor cortices during unilateral finger tapping. It is thus possible that the asymmetry effects become visible especially when comparing large polls of subjects in the left against subjects in the right hand contraction conditions.

Alpha asymmetries between the two brain hemispheres were also not systematically modified after hand contractions, meaning that regardless of general changes in activity levels at each phase, relative activity between homolog locations at each side remained constant. This observation is especially relevant regarding anterior brain asymmetries, which are known to influence mood and emotional predispositions [67– 69]. While left anterior asymmetries at rest (smaller left alpha amplitudes) are associated with tendencies towards parasympathetic activation, approach behavior, and positive affect [67–69], right sided asymmetries are related with sympathetic activation, avoidance behavior, and negative affect [67–69]. In EEG emotion research, anterior asymmetries are most commonly assessed between electrodes F3 on the left and F4 on the right [68–70], which tap on activity of the dorsolateral pre-frontal cortex as part of a broader emotional regulation system [68, 70, 71]. In our sample, these electrode pairs consistently showed greater left sided activity (smaller left alpha amplitudes, Fig 1). Other electrode pairs used in emotion research such as FC3-FC4 [68], and C3-C4 [67, 72] also kept constant left sided asymmetry throughout our experiment. These constant asymmetry levels suggest that left hand contractions might be safely used to enhance alpha amplitudes without the risk of inducing a potentially unwanted right-sided frontal asymmetry.

In sum, our results suggest that unilateral hand contractions result in a state of reduced cortical activity (and not the persistent activation asymmetry) after their termination, which is more pronounced if the left hand was used. This seems to be a plausible mechanism underlying the subsequent behavioral effects reported in previous experiments [1–7]. Consistent with this, prior laboratory research reports that elevated alpha levels at rest (indicating cortical inhibition) improve the brain's engagement in subsequent information processing [12–15]. Research in sport and rehabilitation performance further supports that global reductions in basal cortical activity facilitate task-specific activations and reduce competition from non-essential cortical regions [16–21, 73]. The present experiment included no tasks following hand contractions in order to prevent task-related activations to affect the measurement. Future studies should attempt to include a test of the mediating effect of induced alpha enhancement on subsequent behavior.

Conclusions

The current experiment tested the state of cortical activity during and after unilateral hand contractions. The EEG reported alpha band assessment revealed that hand contractions produce bilateral activations of the motor cortex during their execution. But after contractions, a state of globally reduced cortical activity emerges, especially when the left hand was used. This state is most likely produced by inhibitory mechanisms activated during repetitive contractions, which outlast their termination. It may be proposed that once this state is induced, it facilitates performance in subsequent tasks by facilitating task-specific cortical activations and preventing interference from other, nonessential cortical regions. In addition, the increase of amplitudes in the alpha range through hand contractions is similar to that induced through other techniques like repetitive transcranial magnetic stimulation [29] or transcranial alternating current stimulation [22, 30]. Therefore, unilateral hand contractions, especially with the left hand, also show promissory possibilities for their use in clinical settings.

Supporting Information

S1 Annex. Differences between visual and sensorimotor regions during contractions.
(DOCX)

S2 Annex. Alternative Electrode Referencing.
(DOCX)

S1 Fig. Comparison of alpha amplitudes before and after contractions of each hand for each subgroup. A) Left-first subgroup, left contractions. B) Left-first subgroup, right contractions. C) Right-first subgroup, left contractions. D) Right-first subgroup, right contractions.
(TIF)

S2 Fig. Highlight of occipital effects observed during contractions. A) For the left hand-block. B) For the right hand-block. The plot is taken from Fig 1 with highlights for occipital electrodes. The accompanying difference maps are obtained by subtracting the phase during contractions from the baseline. The scale has been adjusted to illustrate occipital effects.
(TIF)

S3 Fig. Average Reference plot of the alpha amplitudes at each electrode before, during and after contractions. A) For the left hand-block. B) For the right hand-block. Accompanying difference maps indicate the distribution of amplitude changes on the scalp when subtracting the baseline before contractions from the phases during and after contractions.
(TIF)

S4 Fig. Surface Laplacian plot of the alpha amplitudes at each electrode before, during and after contractions. A) For the left hand-block. B) For the right hand-block. Accompanying difference maps indicate the distribution of amplitude changes on the scalp when subtracting the

baseline before contractions from the phases during and after contractions.
(TIF)

S1 Table. Mean (*SD*) alpha amplitudes at each electrode before left and right contractions with *t*-scores and effect sizes for differences between both baselines.
(DOCX)

S2 Table. *t*-scores and effect sizes for differences in alpha amplitudes between the phases before and after hand contractions for each electrode and each hand according to which hand-block was performed first.
(DOCX)

Author Contributions

Conceived and designed the experiments: FCV MD PG JB. Performed the experiments: FCV. Analyzed the data: FCV PG MD JB. Contributed reagents/materials/analysis tools: JB. Wrote the paper: FCV PG JB MD.

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S1 Table. Mean (*SD*) alpha amplitudes at each electrode before left and right contractions with *t*-scores and effect sizes for differences between both baselines.

Electrode Position	**Before Left Contractions**	**Before Right Contractions**	***t*(19)**	d_z
Fp1	1.62 (.48)	1.75 (.59)	-2.29*	.51
Fp2	1.59 (.47)	1.72 (.54)	-2.15*	.48
F3	1.76 (.59)	1.86 (.67)	-2.27*	.51
F4	1.78 (.55)	1.91 (.64)	-2.99**	.67
F7	1.66 (.54)	1.77 (.65)	-2.39*	.53
F8	1.66 (.50)	1.75 (.60)	-1.91	.43
C3	1.90 (.61)	1.99 (.66)	-1.63	.36
C4	1.94 (.64)	2.06 (.66)	-2.12*	.47
FC3	1.78 (.57)	1.89 (.62)	-2.14*	.48
FC4	1.81 (.54)	1.92 (.60)	-2.60*	.58
FT7	1.61 (.57)	1.68 (.63)	-.90	.20
FT8	1.54 (.54)	1.62 (.60)	-1.33	.30
CP3	2.06 (.65)	2.13 (.66)	-1.24	.28
CP4	2.11 (.75)	2.21 (.71)	-1.62	.36
T7	1.45 (.59)	1.56 (.55)	-1.37	.31
T8	1.42 (.62)	1.50 (.65)	-.77	.17
P7	2.08 (.73)	2.16 (.75)	-1.35	.30
P8	2.05 (.73)	2.18 (.74)	-1.86	.42
P3	2.21 (.74)	2.31 (.75)	-1.44	.32
P4	2.19 (.74)	2.30 (.72)	-1.50	.34
O1	2.35 (.78)	2.50 (.96)	-1.43	.32
O2	2.32 (.81)	2.46 (.93)	-1.72	.38

*indicates significance $p < .05$, and **indicates significance $p < .01$.

S2 Table. *t*-scores and effect sizes for differences in alpha amplitudes between the phases before and after hand contractions for each electrode and each hand according to which hand-block was performed first.

Electrode Position	**Left Hand-Block First**				**Right Hand-Block First**			
	Left Hand		**Right Hand**		**Left Hand**		**Right Hand**	
	***t*(9)**	**d_z**	***t*(9)**	**d_z**	***t*(9)**	**d_z**	***t*(9)**	**d_z**
Fp1	-2.78*	.88	-.02	.01	-2.22	.70	-1.79	.57
Fp2	-2.72*	.86	.42	.13	-1.98	.63	-.84	.27
F3	-3.12*	.99	-.27	.09	-2.54*	.80	-2.36*	.75
F4	-2.75*	.87	-.04	.01	-2.37*	.75	-1.77	.56
F7	-2.38*	.75	-1.12	.35	-2.32*	.73	-1.84	.58
F8	-1.30	.41	-.19	.06	-2.24*	.71	-1.51	.48
C3	-2.27*	.72	-1.90	.60	-2.41*	.76	-.19	.06
C4	-3.10*	.98	-.94	.30	-2.95*	.93	-.98	.31
FC3	-2.86*	.90	-1.08	.34	-2.28*	.72	-.31	.10
FC4	-2.79*	.88	-.98	.31	-2.72*	.86	.04	.01
FT7	-2.29*	.72	-1.67	.53	-2.84*	.90	-1.10	.35
FT8	-2.51*	.79	-.71	.22	-2.81*	.89	-.67	.21
CP3	-2.50*	.79	-.78	.25	-2.73*	.86	-.56	.18
CP4	-3.57**	1.13	-1.44	.46	-2.95*	.93	-1.66	.52
T7	-1.48	.47	-1.39	.44	-3.43**	1.08	-1.00	.32
T8	-1.68	.53	-1.86	.59	-3.51**	1.11	-1.57	.50
P7	-2.09	.66	-.56	.18	-2.67*	.84	-2.72*	.86
P8	-3.12*	.99	-1.82	.58	-2.44*	.77	-3.56**	1.13
P3	-3.45**	1.09	-.43	.14	-2.61*	.83	-1.30	.41
P4	-3.61**	1.14	-1.74	.55	-2.89*	.91	-1.83	.58
O1	-3.19*	1.01	-1.05	.33	-1.82	.58	-2.52*	.80
O2	-3.34**	1.06	-1.73	.55	-2.31*	.73	-2.59*	.82

*indicates significance $p < .05$, and **indicates significance $p < .01$.

S1 ANNEX. Differences between visual and sensorimotor regions during contractions.

An interaction between electrode and phase indicated that differences among electrodes varied at each phase. In part, this owes to the fact that electrodes C3, C4, CP3, and CP4, which reflect sensorimotor areas, showed the greatest bilateral decrease in alpha amplitudes during contractions (see Table 1 and Table 2 in the main text). On the other side, electrodes O1 and O2, reflecting visual areas, slightly increased their amplitudes during contractions, except for O2 for the right hand, which slightly decreased (Table 1 in the main text). Such a contrast between central and occipital electrodes enhanced their differences during contractions. To better visualize this contrast, Figure S2 displays the same difference maps of Figure 1 with an adjusted scale to enhance the slight increase of alpha amplitude in occipital regions.

For post-hoc analysis, the differences between electrodes O1 and O2 with each of the other electrodes were calculated at each phase for each hand. Afterwards, the obtained differences at each phase were compared with each other using *t*-tests. For the left hand, Table A in this supplement shows the obtained difference values at each phase and Table B shows the *t*-values obtained when those differences are compared to each other. For the right hand, Table C displays the differences, and Table D the results of the comparisons between those differences.

As can be observed in Table B for the left hand and Table D for the right hand, the difference between occipital electrodes and central electrodes during contractions is consistently greater than that before contractions, as well as after contractions. Further, when comparing the difference among these electrodes after contractions with that before contractions, this discrepancy disappears. The described pattern was observed with the greatest consistency only between occipital and central electrodes for both hands. With occipital vs parietal electrodes the pattern was less consistent, and with other electrodes is not observed.

This observation is in line with the findings reported by Pfurtscheller and Lopes da Silva [47], who used event-related synchronization/desynchronization (ERS/ERD) of the alpha band to observe a simultaneous activation of motor areas and deactivation of the visual areas over the scalp during hand movements.

Table A

	Mean Differences					
	O1			O2		
	Before	During	After	Before	During	After
C3	.45 (.45)	.73 (.77)	.51 (.59)	.42 (.52)	.70 (.77)	.50 (.62)
C4	.41 (.37)	.68 (.66)	.47 (.55)	.38 (.44)	.64 (.67)	.46 (.59)
CP3	.29 (.41)	.62 (.73)	.34 (.53)	.26 (.50)	.59 (.74)	.32 (.61)
CP4	.24 (.31)	.57 (.60)	.29 (.45)	.21 (.39)	.54 (.61)	.28 (.51)
Fp1	.73 (.44)	.92 (.68)	.83 (.66)	.70 (.49)	.88 (.68)	.82 (.66)
Fp2	.76 (.44)	.93 (.71)	.88 (.66)	.72 (.48)	.90 (.70)	.87 (.65)
F3	.60 (.40)	.77 (.69)	.67 (.56)	.56 (.46)	.74 (.69)	.65 (.59)
F4	.57 (.42)	.74 (.72)	.66 (.58)	.54 (.49)	.70 (.72)	.65 (.61)
F7	.69 (.42)	.83 (.68)	.75 (.51)	.66 (.47)	.80 (.68)	.74 (.55)
F8	.69 (.45)	.85 (.73)	.82 (.65)	.66 (.52)	.82 (.73)	.81 (.68)
FC3	.57 (.41)	.78 (.79)	.63 (.57)	.54 (.49)	.74 (.78)	.62 (.61)
FC4	.55 (.40)	.70 (.70)	.62 (.57)	.51 (.47)	.66 (.70)	.61 (.60)
FT7	.74 (.41)	.89 (.77)	.79 (.58)	.71 (.47)	.86 (.77)	.78 (.63)
FT8	.81 (.51)	.91 (.81)	.91 (.70)	.78 (.57)	.87 (.83)	.90 (.74)
T7	.90 (.43)	1.05 (.77)	.95 (.52)	.87 (.48)	1.01 (.78)	.94 (.57)
T8	.93 (.60)	1.01 (.78)	.99 (.70)	.90 (.67)	.98 (.80)	.97 (.78)
P7	.27 (.30)	.51 (.52)	.32 (.37)	.24 (.39)	.47 (.54)	.31 (.53)
P8	.30 (.39)	.45 (.44)	.29 (.40)	.27 (.46)	.42 (.47)	.28 (.48)
P3	.14 (.29)	.40 (.48)	.18 (.40)	.11 (.37)	.36 (.49)	.16 (.50)
P4	.16 (.24)	.36 (.40)	.17 (.39)	.13 (.32)	.32 (.39)	.16 (.42)

Mean (SD) of the differences in alpha amplitudes between electrodes O1 and O2 and the rest of the electrodes across each measuring phase for the left hand-block.

Table B

	t-scores					
	O1			O2		
	Before vs During	During vs After	Before vs After	Before vs During	During vs After	Before vs After
C3	-2.25*	2.21*	-1.00	-2.51*	2.06	-1.84
C4	-2.30*	2.39*	-.66	-2.61*	2.13*	-1.18
CP3	-2.71*	2.82*	-.68	-2.97*	2.42*	-1.21
CP4	-2.47*	3.01*	-.52	-2.70*	2.57*	-.94
Fp1	-1.73	0.94	-1.25	-2.02	0.76	-2.13*
Fp2	-1.69	0.62	-1.61	-2.00	0.39	-2.67*
F3	-1.60	1.28	-1.01	-1.83	1.05	-1.86
F4	-1.59	0.98	-1.44	-1.82	0.70	- 2.54
F7	-1.28	0.92	-1.06	-1.48	0.73	-2.37*
F8	-1.56	0.41	-1.69	-1.84	0.09	-2.61
FC3	-1.73	1.80	-0.98	-1.95	1.49	-1.80
FC4	-1.54	1.02	-1.09	-1.77	0.74	-2.02
FT7	-1.28	1.31	-0.71	-1.43	1.05	-1.27
FT8	-0.91	-0.05	-1.27	-1.01	-0.36	-1.98
T7	-1.05	0.94	-0.57	-1.15	0.74	-1.10
T8	-0.72	0.39	-0.63	-0.81	0.08	-1.11
P7	-2.39*	2.51*	-.87	-2.72*	1.80	-1.30
P8	-2.48*	2.76*	.21	-3.13*	2.52*	-.241
P3	-2.58*	2.70*	-.60	-2.79*	2.03	-1.01
P4	-2.39*	2.82*	-.21	-2.73*	1.76	-.68

t-scores for differences in the disparity of electrodes O1 and O2 against other electrodes during the recording phases compared to each other during the left hand-block.

*indicates significance $p < .05$ (uncorrected), and **indicates significance $p < .001$ (uncorrected).

Table C

	Mean Differences					
	O1			O2		
	Before	During	After	Before	During	After
C3	.51 (.58)	.78 (.82)	.57 (.66)	.47 (56)	.80 (.79)	.55 (.67)
C4	.43 (.52)	.71 (.72)	.48 (.50)	.40 (.54)	.72 (.72)	.47 (.55)
CP3	.36 (.55)	.68 (.82)	.41 (.62)	.32 (.56)	.70 (.80)	.40 (.64)
CP4	.29 (.45)	.55 (.64)	.28 (.44)	.25 (.47)	.57 (.64)	.27 (.49)
Fp1	.75 (.53)	.88 (.68)	.83 (.53)	.71 (.55)	.90 (.69)	.81 (.60)
Fp2	.78 (.53)	.92 (.71)	.89 (.55)	.74 (.54)	.93 (.72)	.87 (.60)
F3	.63 (.49)	.77 (.67)	.69 (.50)	.60 (.52)	.78 (.66)	.68 (.57)
F4	.59 (.54)	.73 (.72)	.67 (.56)	.55 (.57)	.74 (.74)	.66 (.64)
F7	.72 (.48)	.82 (.64)	.76 (.46)	.69 (.51)	.83 (.65)	.75 (.54)
F8	.75 (.58)	.84 (.72)	.82 (.60)	.71 (.59)	.85 (.74)	.81 (.66)
FC3	.61 (.53)	.79 (.75)	.68 (.58)	.57 (.54)	.80 (.73)	.67 (.62)
FC4	.58 (.56)	.75 (.77)	.67 (.60)	.54 (.57)	.76 (.76)	.66 (.64)
FT7	.82 (.54)	.90 (.77)	.81 (.55)	.78 (.55)	.91 (.76)	.79 (.59)
FT8	.87 (.66)	.96 (.81)	.94 (.66)	.84 (.66)	.97 (.83)	.92 (.71)
T7	.94 (.52)	1.04 (.81)	.92 (.58)	.90 (.52)	1.05 (.79)	.91 (.61)
T8	1.00 (.65)	1.08 (.80)	.96 (.66)	.96 (.67)	1.09 (.82)	.95 (.72)
P7	.33 (.34)	.52 (.50)	.33 (.35)	.29 (.41)	.53 (.53)	.32 (.46)
P8	.31 (.42)	.41 (.44)	.26 (.45)	.28 (.44)	.42 (.46)	.24 (.50)
P3	.19 (.44)	.44 (.62)	.22 (.42)	.15 (.46)	.45 (.60)	.20 (.46)
P4	.20 (.41)	.32 (.45)	.18 (.41)	.16 (.40)	.33 (.43)	.17 (.43)

Mean (SD) of the differences in alpha amplitudes between electrodes O1 and O2 and the rest of the electrodes across each measuring phase for the right hand-block.

Table D

	t-scores					
	O1			O2		
	Before vs During	During vs After	Before vs After	Before vs During	During vs After	Before vs After
C3	-2.58*	2.11*	-1.15	-3.03*	2.36*	-1.58
C4	-2.90*	2.16*	-1.02	-3.03*	2.44*	-1.51
CP3	-2.73*	2.50*	-.89	-3.03*	2.79	-1.22
CP4	-2.59*	2.30*	.09	-2.88*	2.69*	-.472
Fp1	-1.80	0.83	-3.17*	-2.18*	1.12	-3.12*
Fp2	-1.90	0.46	-4.24**	-2.30*	0.78	-4.07**
F3	-1.65	0.99	-1.57	-2.07	1.27	-1.93
F4	-2.02	0.87	-2.54*	-2.34*	1.12	-3.14*
F7	-1.31	0.79	-1.17	-1.80	1.10	-1.64
F8	-1.56	0.33	-2.32*	-1.93	0.66	-2.66*
FC3	-2.25*	1.29	-1.78	-2.74*	1.61	-2.14*
FC4	-2.30*	1.04	-2.96*	-2.58*	1.30	-3.38*
FT7	-1.05	1.02	0.19	-1.56	1.31	-0.21
FT8	-1.20	0.26	-1.26	-1.59	0.56	-1.68
T7	-0.88	0.92	0.19	-1.31	1.11	-0.20
T8	-1.09	1.22	0.59	-1.53	1.39	0.20
P7	-2.39*	2.08	-.08	-2.51*	2.12*	-.585
P8	-1.70	2.29*	1.67	-2.73*	3.08*	.95
P3	-2.38*	2.22*	-.729	-2.67*	2.52*	-1.14
P4	-1.55	1.32	.479	-2.43*	1.71	-.29

t-scores for differences in the disparity of electrodes O1 and O2 against other electrodes during the recording phases compared to each other during the right hand-block.
*indicates significance *p* < .05 (uncorrected), and **indicates significance *p* < .001 (uncorrected).

S2 ANNEX. Alternative Electrode Referencing

In order to corroborate the results obtained with the linked mastoids reference, the data was further analyzed using an average-reference scheme, and a reference-free surface Laplacian approach.

Average Reference

The average reference procedure showed results that largely mirrored those obtained with a linked-mastoids reference, with main effects of phase $F(2, 38) = 22.88$, $p = .001$, $\eta_p^2 = .55$ and electrode $F(21, 399) = 28.96$, $p = .001$, $\eta_p^2 = .60$; no significant effect for hand-block $F(1, 19) = .598$, $p = .45$, $\eta_p^2 = .03$; an interaction between electrode and phase, $F(42, 798) = 8.23$, $p = .001$, $\eta_p^2 = .30$; and no significant three way interaction between all factors $F(42, 798) = .68$, $p = .937$, $\eta_p^2 = .04$.

The interaction between phase and hand-block however, did not reach statistical significance $F(2, 38) = 2.43$, $p = .101$, $\eta_p^2 = .11$. Post-hoc *t*-tests comparing the value of each electrode at each phase (Table A in this supplement) showed that although alpha amplitudes increased after left-hand contractions compared to baseline (S3 Figure), fewer electrodes reached statistical significance, or they did to a lesser degree.

As with the linked-mastoids reference, a repeated measures ANOVA with the asymmetry ratios showed no main effects and there was no significant interaction between phase and hand-block $F(2, 38) = .21$, $p = .814$, $\eta_p^2 = .01$, confirming that alpha asymmetry ratios were not affected my hand contractions.

Table A.

Electrode Position	**Left Hand Contractions**				**Right Hand Contractions**			
	Before vs. During		**Before vs. After**		**Before vs. During**		**Before vs. After**	
	***t*(19)**	d_z	***t*(19)**	d_z	***t*(19)**	d_z	***t*(19)**	d_z
Fp1	3.03*	.68	-2.92*	.65	2.49	.56	-.41	.09
Fp2	2.94*	.66	-2.17	.49	2.96*	.66	.34	.08
F3	3.78**	.85	-3.51**	.78	2.61	.58	-.59	.13
F4	2.99*	.67	-2.38	.53	3.04*	.68	-.03	.01
F7	2.33	.52	-3.00*	.67	2.01	.45	-1.11	.25
F8	2.18	.49	-1.47	.33	2.17	.49	-.80	.18
C3	4.44**	.99	-2.46	.55	3.92**	.88	-.18	.04
C4	4.10**	.92	-2.59*	.58	4.25**	.95	-.77	.17
FC3	3.16*	.71	-3.09*	.69	3.17**	.71	-.12	.03
FC4	2.91*	.65	-2.49	.56	3.23**	.72	.43	.10
FT7	2.17	.49	-3.69**	.83	2.21	.49	-1.47	.33
FT8	1.98	.44	-2.95*	.66	2.04	.46	-1.37	.31
CP3	5.31**	1.19	-2.28	.51	4.50**	1.01	.01	.00
CP4	4.36**	.97	-3.40**	.76	5.07**	1.13	-1.77	.40
T7	2.39	.53	-3.60**	.80	2.29	.51	-1.18	.26
T8	1.59	.36	-4.11**	.92	2.08	.47	-3.27**	.73
P7	3.16*	.71	-3.43**	.77	2.82*	.63	-1.00	.22
P8	1.18	.26	-4.06**	.91	1.21	.27	-4.92**	1.10
P3	3.72**	.83	-2.75*	.61	4.10**	.92	-.23	.05
P4	2.40	.54	-4.16**	.93	2.99*	.67	-1.96	.44
O1	-0.27	.06	-2.30	.51	0.14	.03	-1.02	.23
O2	-0.46	.10	-3.18**	.71	-0.45	.10	-2.38	.53

t-scores and effect sizes for differences in alpha amplitudes between the phases before and during and the phases before and after hand contractions for each electrode and each hand using Average Reference. *indicates significance $p < .016$, and **indicates significance $p < .003$ (corrected for multiple (3) comparisons – Bonferroni).

Surface Laplacian

A surface Laplacian [38] was further implemented. Given the observed widespread increase of alpha amplitudes after left contractions with the linked mastoids and average references, a spline order $m = 7$ and smoothing constant $\lambda = 0.00001$ were used for the surface Laplacian [39]. These parameters, should prevent high-pass spatial filtering by the surface Laplacian and hence emphasize global over local features of the EEG [39-42] such as the current widespread increase of alpha amplitudes.

The results coincided with the linked-mastoid reference, showing main effects of phase $F(2, 38) = 18.84$, $p = .001$, $\eta_p^2 = .50$ and electrode $F(21, 399) = 31.36$, $p = .001$, $\eta_p^2 = .62$; no significant effect for hand-block $F(1, 19) = 1.08$, $p = .311$, $\eta_p^2 = .05$; an interaction between electrode and phase, $F(42, 798) = 7.24$, $p = .001$, $\eta_p^2 = .28$; and no significant three way interaction $F(42, 798) = .430$, $p = .999$, $\eta_p^2 = .02$.

Most importantly, the interaction between phase and hand-block was significant $F(2, 38) = 3.29$, $p = .048$, $\eta_p^2 = .15$, as with linked-mastoids. Post-hoc *t*-tests in Table B of this supplement show that while all electrodes except for CP3 show a significant increase in alpha amplitudes after left hand contractions (S4 Figure), only electrode P8 does so after right hand contractions.

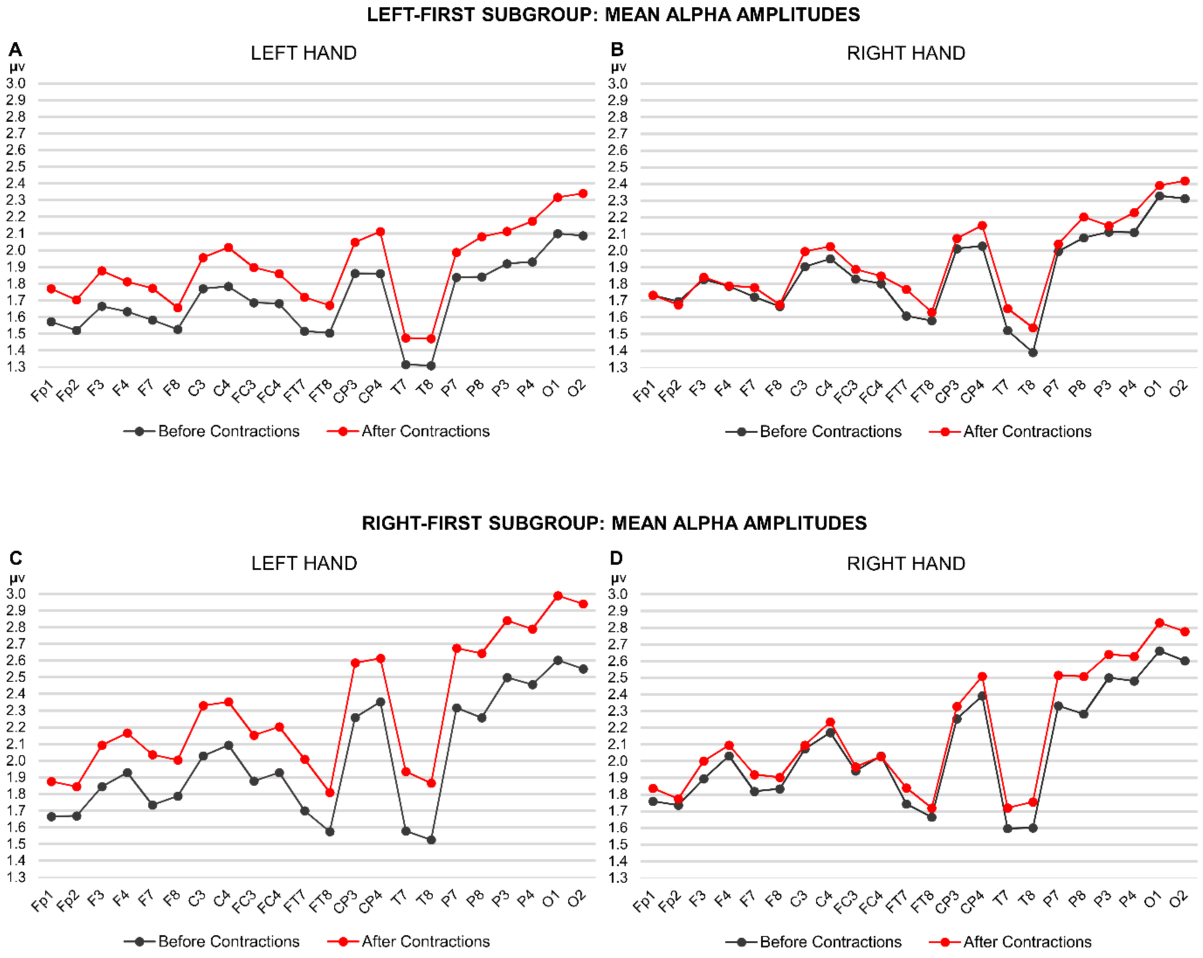
As with the linked-mastoids reference, a repeated measures ANOVA with the asymmetry ratios showed no main effects and there was no significant interaction between phase and hand-block $F(2, 38) = .76$, $p = .468$, $\eta_p^2 = .04$, confirming that alpha asymmetry ratios were not affected my hand contractions.

Table B.

Electrode Position	**Left Hand Contractions**				**Right Hand Contractions**			
	Before vs. During		**Before vs. After**		**Before vs. During**		**Before vs. After**	
	***t*(19)**	d_z	***t*(19)**	d_z	***t*(19)**	d_z	***t*(19)**	d_z
Fp1	5.12**	1.14	-3.71**	.83	4.94**	1.10	-.33	.07
Fp2	4.18**	.93	-4.64**	1.04	4.59**	1.03	-1.53	.34
F3	4.34**	.97	-3.34**	.75	4.27**	.95	.05	.01
F4	2.40	.54	-3.93**	.88	3.23**	.72	-1.09	.24
F7	0.97	.22	-3.08*	.69	1.73	.39	.34	.08
F8	-0.10	.02	-3.64**	.81	0.39	.09	-1.41	.32
C3	2.96*	.66	-2.94*	.66	3.11*	.70	-.87	.19
C4	2.50	.56	-2.95*	.66	2.99*	.67	-1.11	.25
FC3	2.37	.53	-3.08*	.69	2.49	.56	-.41	.09
FC4	1.42	.32	-3.30**	.74	2.11	.47	-.89	.20
FT7	1.07	.24	-3.25**	.73	1.33	.30	-.48	.11
FT8	0.30	.07	-4.28**	.96	0.71	.16	-1.83	.41
CP3	4.48**	1.00	-2.63*	.59	4.43**	.99	-.70	.16
CP4	3.37**	.75	-3.21**	.72	4.20**	.94	-1.30	.29
T7	2.86*	.64	-3.51**	.78	2.64*	.59	-1.05	.23
T8	2.27	.51	-5.24**	1.17	2.78*	.62	-2.27	.51
P7	3.62**	.81	-3.02*	.68	4.14**	.93	-.51	.11
P8	2.69*	.60	-4.59**	1.03	3.54**	.79	-2.80*	.63
P3	4.01**	.90	-2.70*	.60	4.10**	.92	-.35	.08
P4	2.67*	.60	-3.87**	.87	3.21**	.72	-1.72	.38
O1	0.63	.14	-2.96*	.66	0.92	.21	-1.01	.23
O2	0.10	.02	-3.44**	.77	0.06	.01	-2.51	.56

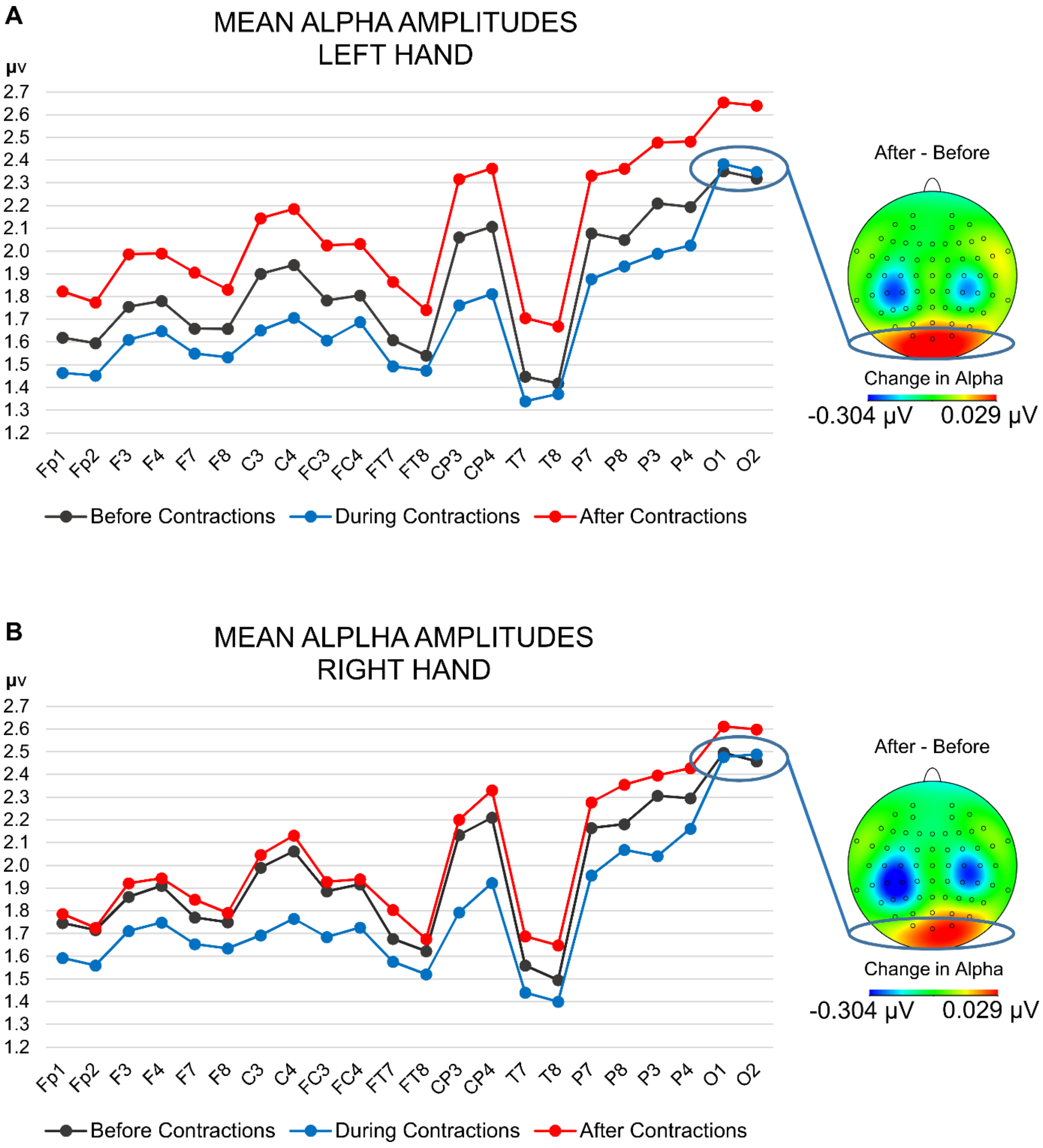
t-scores and effect sizes for differences in alpha amplitudes between the phases before and during and the phases before and after hand contractions for each electrode and each hand.
*indicates significance $p < .016$, and **indicates significance $p < .003$ (corrected for multiple (3) comparisons – Bonferroni).

S1 FIG



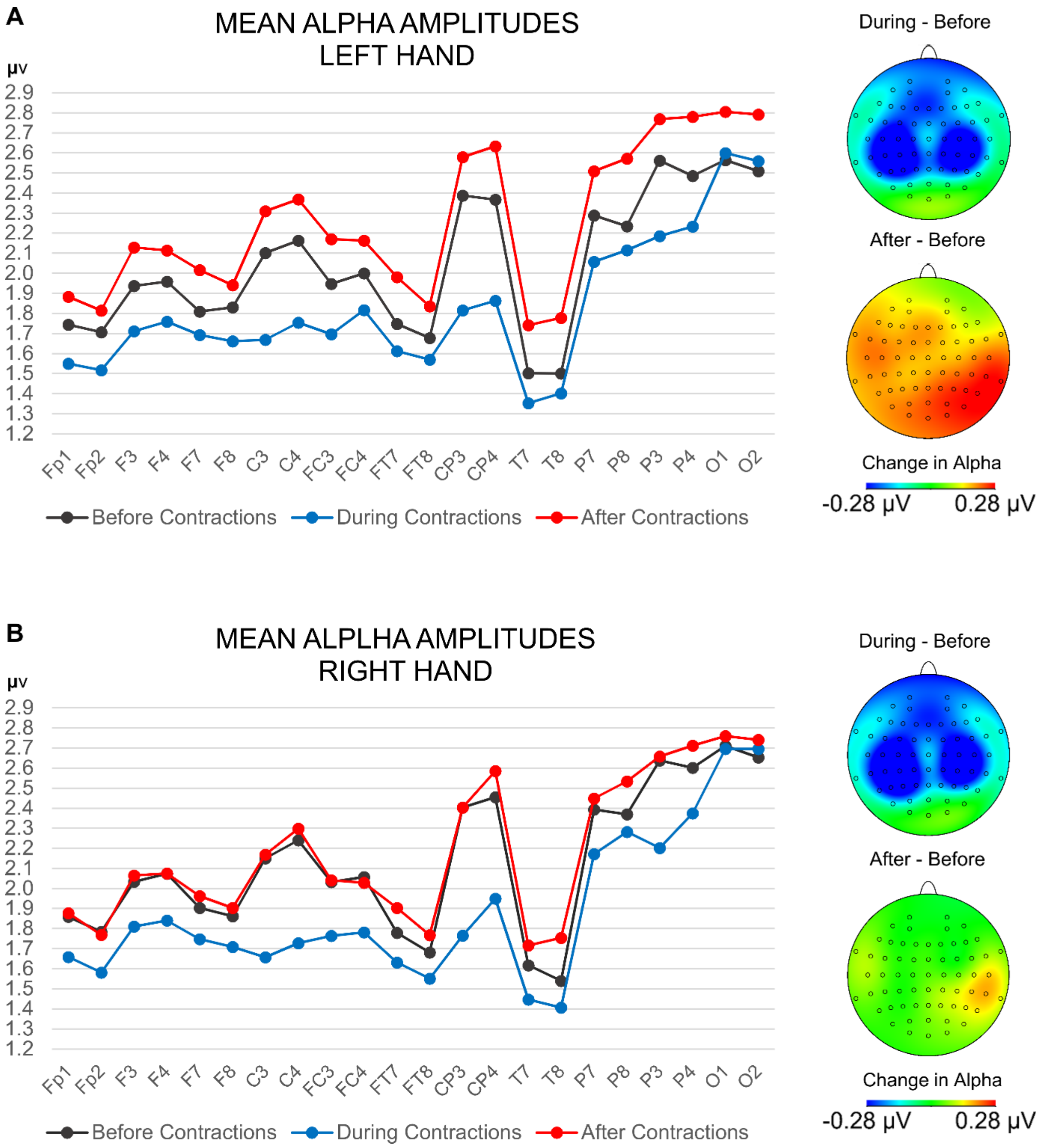
S1 Fig. Comparison of alpha amplitudes before and after contractions of each hand for each subgroup. A) Left-first subgroup, left contractions. B) Left-first subgroup, right contractions. C) Right-first subgroup, left contractions. D) Right-first subgroup, right contractions.

S2 FIG



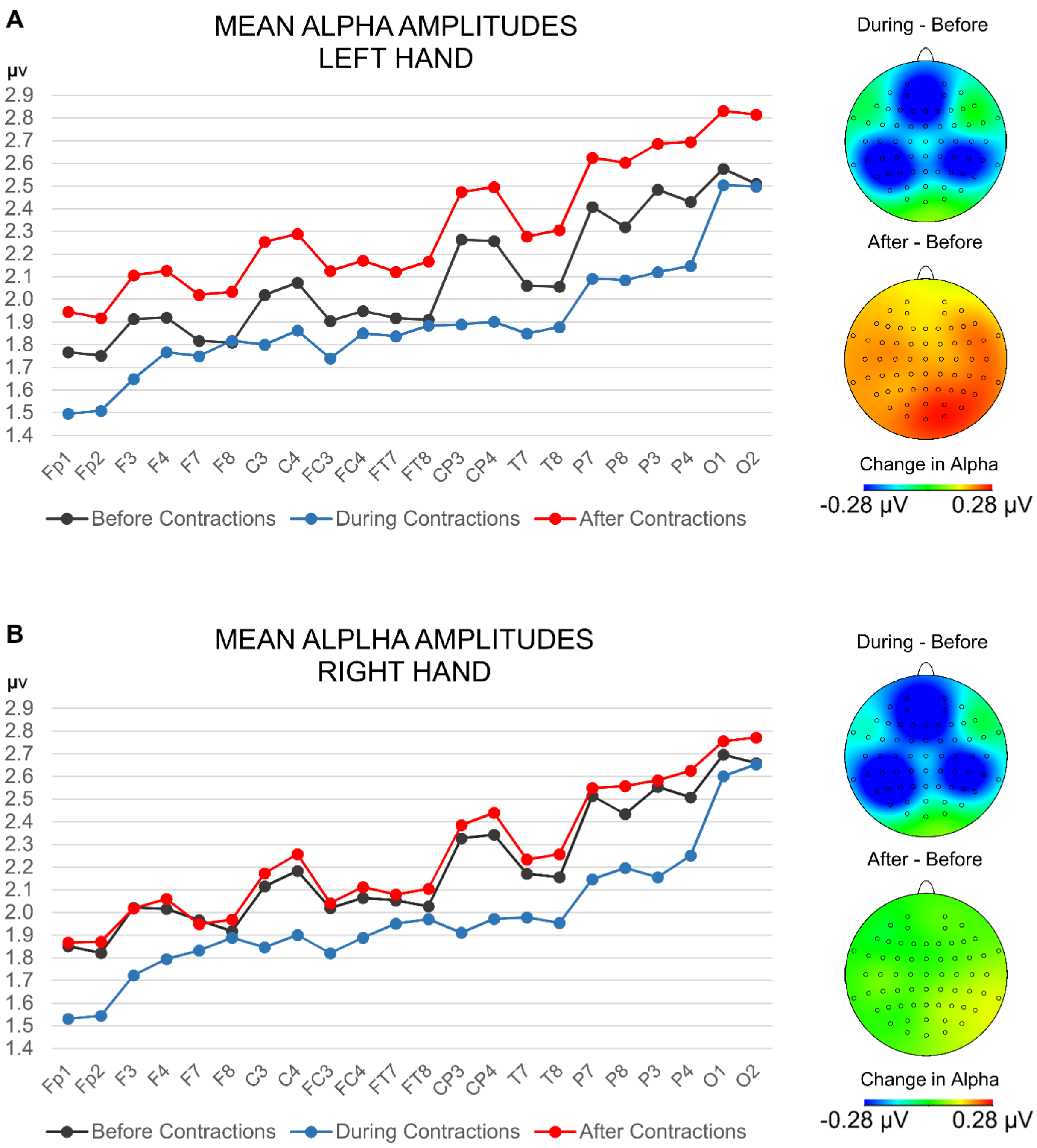
S2 Fig. Highlight of occipital effects observed during contractions. A) For the left hand-block. B) For the right hand-block. The plot is taken from Fig 1 with highlights for occipital electrodes. The accompanying difference maps are obtained by subtracting the phase during contractions from the baseline. The scale has been adjusted to illustrate occipital effects.

S3 FIG



S3 Fig. Average Reference plot of the alpha amplitudes at each electrode before, during and after contractions. A) For the left hand-block. B) For the right hand-block. Accompanying difference maps indicate the distribution of amplitude changes on the scalp when subtracting the baseline before contractions from the phases during and after contractions.

S4 FIG



S4 Fig. Surface Laplacian plot of the alpha amplitudes at each electrode before, during and after contractions. A) For the left hand-block. B) For the right hand-block. Accompanying difference maps indicate the distribution of amplitude changes on the scalp when subtracting the baseline before contractions from the phases during and after contractions.

Chapter 3

Theta amplitude as an indicator of performance proficiency in a dynamic visuospatial task[2]

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[2] Manuscript for submission for journal submission.

Theta amplitude as an indicator of performance proficiency in a dynamic visuospatial task

Abstract

Dynamic visuospatial tasks, which require a continuous engagement of attention over long periods have been little studied with the electroencephalogram (EEG). Specifically, the role of the EEG theta band in these tasks is not clear, with theta enhancements improving performance in some studies, and hindering it in others. In the current study, 30 participants performed the Pong videogame as a dynamic visuospatial task to analyze the influence of theta, as well as the alpha band amplitude and its asymmetry ratio on performance. The theta band showed a significant increase at central parietal regions, which correlated negatively with performance, especially at anterior regions. The alpha band showed a significant decrease, greater at right over left parietal regions, but neither the amplitude nor the asymmetry ratio correlated with task performance. With theta being an indicator of top-down cognitive control, we conclude that proficient performance in dynamic visuospatial tasks depends on a bottom-up guidance of attention with little top-down intervention.

3.1 INTRODUCTION

In the present electroencephalogram (EEG) study, we used the alpha and theta bands to analyze the role of hemispheric activation asymmetry and top-down cognitive control on performance in a dynamic visuospatial task, the videogame “Pong”. The Pong game is a 2-D electronic table tennis game, in which a player uses two in-game paddles to hit a ball back and forth. This kind of dynamic tasks in the laboratory serves as an approximation to scenarios where neurophysiological measures are difficult or impossible to assess, such as dynamic sports (Janelle & Hatfield, 2008), machinery operation (Touryan et al., 2016; Borghini et al., 2014), or military settings (Kerick et al., 2007; Janelle & Hatfield, 2008). In contrast to discrete visuospatial tasks (e.g., marksmanship), dynamic visuospatial tasks such as the Pong game have been very little studied with EEG. The aim of the present work therefore was to explore the effects of alpha and theta amplitudes on performance in the Pong game.

Dynamic visuospatial tasks differ from discrete visuospatial tasks in their demands on engagement and continuous attention. Discrete, self-paced tasks are characterized by self-paced isolated trials, as in rifle and pistol shooting (Haufler et al., 2000; Kerick et al., 2004), archery (Landers et al., 1994; Salazar et al., 1990), or golf putting (Crews et al., 1993), where a participant can disengage attention after each trial and re-engage before the next. In contrast, dynamic tasks require continuous attention and constant engagement in order to monitor the visual scene and react accordingly (Janelle & Hatfield, 2008; Kerick et al., 2007; Kramer, 2007; Fournier et al., 1999). Examples of studied dynamic visuospatial tasks are video games (Rebert & Low, 1978; Rebert et al., 1984; Kramer, 2007), driving (Borghini et al., 2012; Touryan et al., 2016), radar operation (Beatty et al., 1974) or non-self-paced shooting (Kerick et al., 2007).

Both dynamic and discrete visuospatial tasks require a delicate coordination between cortical areas of the brain in order to achieve precision in performance (Hatfield et al., 2004; Milton et al., 2004). Using the *alpha* band as the inverse of cortical activation (Sauseng et al., 2009; Romei et al., 2008; Klimesch et al. 2006), studies with discrete tasks have consistently found that proficient performance requires an increase of activation in right parietal and temporal areas relative to their left counterparts shortly before each trial (Janelle & Hatfield, 2008; Hatfield et al., 2004). This reflects the activation of areas related to visual processing and a simultaneous attenuation of other areas non-essential for the task before implementing an action (Janelle & Hatfield, 2008; Hatfield et al., 2004; Del Percio et al., 2009). Studies with dynamic tasks revealed similar results. Kramer (2007) assessed EEG at left and right temporal leads while participants played a simple 2-D driving game where the player should avoid crashing with the edges of a constantly turning runway. Participants who showed a greater enhancement of alpha power over the left temporal hemisphere, reflecting inhibition of the area, were able to avoid crashing for longer times. Rebert & Low (1978) recorded activity at parietal leads, which reflect visual processing, during rallies of the Pong game. Participants had trained the task to mild proficiency one day previous to the test. Greater reduction of alpha power of right parietal areas, reflecting activation of the area, were associated with greater duration of each Pong rally before losing the ball. Hence, findings with the alpha band are consistent between discrete and dynamic visuospatial tasks, both requiring a dominant activation of the right hemisphere over the left, especially at parietal regions.

The role of the *theta* band is less known in discrete and dynamic tasks. The theta band, especially at the fronto-central scalp regions is generally accepted as an indicator of top-down cognitive control over attention, which coordinates different cortical regions and prevents distractions (Cavanagh & Frank, 2014; Anguera et al., 2013; Sauseng et al., 2007; Inanaga, 1998). On self-paced tasks, expert performers in golf putting (Baumeister et al., 2008) and rifle shooting (Doppelmayr et al., 2008; Haufler et al., 2000) have shown to elevate theta power at frontal-central regions a few seconds before action execution, while non-experts do not show such elevation. This theta elevation is thought to reflect an enhancement of focused attention towards the target (Baumeister et al., 2008; Doppelmayr et al., 2008; Haufler et al., 2000). Regarding dynamic tasks, Kerick et al. (2007) tested a reactive shooting task with military personnel who had to discriminate friendly from enemy targets appearing unpredictably. When compared to a shot-only condition, target discrimination elicited a significant theta enhancement at central-parietal regions. According to Kerick et al., the parietal location of the effect reflects an analytic process of visual information towards target identification. Indeed, the theta enhancement was greater in blocks when target exposure times were shorter, reflecting a bigger effort to quickly identify the target. Rebert et al. (1984) with the Pong videogame, observed an enhancement of theta power over central leads and interpreted it as a component of attentional and motor control in the task, but did not explore its relation to performance.

Despite the slightly different scalp location, the theta enhancements in reactive shooting (Kerick et al. 2007) coincide with those in self-paced shooting and golf putting. In particular, greater theta enhancements may allow for better performance because of higher focused attention. However, it is a question whether theta enhancements observed in the Pong game (Rebert et al., 1984) would also improve performance, or otherwise hinder it. Although in both, reactive shooting and Pong, constant vigilance is required, the Pong game requires broad rather than focused attention in order to track the ball, and consequently adjust the paddles. In more complex dynamic tasks such as driving (Touryan et al., 2016; Borghini et al., 2012) or aviation (Borghini et al., 2014), the theta band is used as a marker of cognitive workload which can be caused by exhaustion or complex task requirements, and is detrimental to performance. The Pong game, although simpler than driving or aeroplane operation, is similar in nature to these activities as a dynamic visuospatial task that requires constant attention, updating, and adaptation to circumstances. It is widely supported that visuospatial performance improves when it relies less on cognitive control (Beckmann et al., 2013; Hatfield et al., 2004; Milton et al., 2004). If theta enhancements in dynamic visuospatial tasks represent cognitive workload, it is possible that increases of theta in Pong are detrimental to performance.

In the present study, we used a highly difficult version of the Pong videogame as used by Rebert et al. (1984), with high requirements in prediction of the ball's trajectory, to analyze the effects of alpha asymmetry and central theta amplitude on performance. Whole scalp EEG further allowed to better explore the topographic distribution of these effects. The Pong game can serve as a useful experimental task where variables can be easily manipulated to approximate other more complex dynamic performance scenarios. It does not require a central fixation point; as in Rebert et al. (1984) we used a play field of 7° visual angle to reduce eye movements to a minimum. We additionally tested the reactivity of the alpha band to eye opening or “arrest reaction” (Cheron et al., 2016) as a predictor of subsequent performance in the task.

3.2 MATERIALS AND METHODS

3.2.1 Participants

Thirty six participants were recruited via public advertisement of the study on campus. From these, three showed some tendency towards left-handedness according to the Edinburgh Handedness Inventory (Oldfield et al. 1971) therefore their data was removed, one did not reach training criteria and was not included, and two participants quit the experiment. The final sample consisted of 30 right-handed participants (13 male), with a mean age of 24.8 years (SD = 3.34; range: 19-32 years). Their mean laterality quotient in the Edinburgh Handedness Inventory was +81.14 (range: +60 to +100), laterality quotients range from -100 to +100 and values above 50 indicate strong righthandedness (Oldfield et al. 1971). Before entering the study, the participants were explained the experimental and EEG procedures, assured the confidentiality of their data, and their right to quit the experiment at any time without consequences. Afterwards, the participants signed an informed consent according to the Declaration of Helsinki.

3.2.2 Task and apparatus

"Pong" consists of a 2D electronic table tennis game (Fig 3.1). We used a custom version of Pong with the same paradigm as Rebert & Low (1976) and Rebert et al. (1984), where participants controlled both paddles instead of competing against another player. The aim was to keep the ball in movement for as long as possible on each trial without losing it. Trials lasted for as long as the participant could keep the ball in movement with a top limit of 1 min. Between trials, a 5 s pause ensued, and a warning "Get Ready" signal was displayed for the last 2 s of the pause (Fig 3.1). The paddles were controlled for upward and downward movement respectively with the keyboard keys *w*-*s* for the left, and *p*-*l* for the right paddle. The paddles traveled at constant speed for as long as the corresponding button was pressed. In order to reduce eye movement artifacts on the EEG, the playfield covered 7° visual angle span as in Rebert & Low (1976) and Rebert et al. (1984). The play screen was 11.5 cm, surrounded by a gray background, and participants seated 100 cm away from the screen. Furthermore the swing of the ball from left to right was between 1.3 and 1.6 Hz depending on the ball's trajectory, making slow pursuit eye movements and their corresponding artifact to fall outside the EEG range of interest from 4 Hz onwards. The ball always traveled at constant speed. Each hit with the paddles or the walls produced a "beep" sound. In this version of Pong, difficulty was increased by making the paddles travel much more slowly than the ball, thus making it necessary to predict the ball's end location in advance on top of coordinating the movement of each paddle.

Fig 3.1. Trial sequence in the Pong game. 1) On-screen text "Start with the space-bar" indicated participants to start the game at will. 2) On each trial, participants controlled both paddles with the aim of keeping the ball in movement for as long as possible. A trial ended when the participant lost the ball. 3) After each trial a count of 5 seconds started, on the last two seconds, the counter disappeared and the message "Get Ready" was displayed. 4) After 15 trials, the average trial duration was displayed as feedback to the participant and the block terminated.

3.2.3 Procedure

The experiment was carried in two sessions on separate days. In the first day, participants learned and trained the task. First they practiced for five minutes with a slower version of the game to get acquainted with it. Afterwards they played at normal ball-speed controlling only the left paddle, then the right paddle, and finally both paddles. Before starting with the task at normal speed, the participants were advised to always anticipate the ball, to keep the paddle in the middle, and to try to hit the ball with the center of the paddle to prevent errors. Once the participants were able to control both paddles, they trained until reaching a minimum of 10 s in three non-consecutive trials. During training, trial duration feedback was given after every trial.

The experimental session was carried one or two days afterwards. In the experimental session, the participants first played a 5 min warmup. After EEG preparation, an EEG baseline was recorded, with two minutes eyes closed, and two minutes eyes open. Thereafter, they played two blocks of 15 trials. We currently focus only on the first block, the second consisted of a stress test while playing the game and is currently not reported.

3.2.4 EEG Recording and processing

The EEG data was recorded continuously during the resting baselines and task performance using a Brain Amp amplifier (Brain Products, Munich, Germany) with a band-pass filter from 0.1 to 250 Hz, notch filter enabled at 50 Hz, and a sampling rate of 1000 Hz. The data was obtained with 64 Ag/AgCl active electrode system “actiCAP” (Brain Products, Munich, Germany), placed on an elastic cap (Easy Cap, FMS). All electrodes on the cap are placed according to the international 10/10 system (American Electroencephalographic Society, 1994), referenced to position FCz during recording, with the ground electrode at position AFz. Electrode impedances were kept under 3 kΩ to prevent large impedance differences between homologous sites. Before analysis, all EEG data was up-sampled offline to a power of 2 (1024 Hz) and further filtered between 0.5 and 40 Hz, notch filter enabled at 50 Hz, with an infinite-impulse-response (IIR) filter as implemented in the Brain Vision Analyzer 2 software package (Widmann et al., 2015). All recordings were visually inspected for mechanical artifacts, all segments including artifacts were rejected. Eye movements were corrected through an informax independent component analysis (ICA) as implemented in Brain Vision Analyzer 2 (Makeig et al., 1996; Bell & Seinowski, 1995), removing all high-energy components reflecting blinks and eye movements. Prior to segmentation, the data was converted to a reference-free scheme through a surface Laplacian estimation with a spline order $m = 4$ and smoothing constant $\lambda = 0.00001$. Such parameters were chosen in order to emphasize local over global features of the EEG (Kayser & Tenke, 2015; Tenke & Kayser, 2005), and enhance the subsequent location of theta enhancements and calculation of alpha asymmetries.

EEG recordings were cut into closed eyes and open eyes segments. Pong trials were identified by markers at the beginning and the end of each trial and each one was segmented accordingly. Within each segment, 2 sec contiguous epochs with 50% overlap were created. Spectral amplitudes were extracted through a Fourier transformation using a Hamming Window with 50% overlap between contiguous epochs, resulting in a spectral resolution of 0.5 Hz. All artifact-free epochs were averaged together within the eyes open, eyes closed and Pong playing periods. Amplitudes were extracted for the theta (4 – 7 Hz) and alpha (7 – 12 Hz) bands at all electrodes. For the alpha band, an asymmetry index [right - left/right + left] (Davidson, 1988) was obtained for all homolog electrodes at each side of the scalp except for the midline. In the asymmetry index, positive values indicate greater right sided alpha levels, meaning greater left-sided cortical activity. The alpha asymmetry index is able to identify minor amplitude differences between pairs of homolog electrodes, which could otherwise go undetected during resting state or in bilateral task-related activations (eg. slightly greater right-than-left task-related alpha reductions; Davidson, 1988; Towers & Allen, 2009). Task-related modulation (TRM) of alpha amplitudes, alpha asymmetry and theta amplitudes were derived by subtracting activity during open-eyes baseline from that during the sum of all Pong trials.

3.2.5 Data analyses

Trial duration data was explored to detect possible outliers. In order to identify significant modulations on alpha and theta amplitudes, paired-sample t-tests were implemented for each band comparing the open-eyes baseline and the Pong rallies at each individual electrode. Significant effects are displayed over scalp-maps, using crosses over electrodes significant after Bonferroni correction at the .05 significance level, and dots where significance does not surpass the Bonferroni correction (Woltering et al., 2012). The same procedure was used for the alpha asymmetry ratio at each pair of homolog electrodes. To explore the influence of the EEG markers on performance, Pearson correlations were implemented between trial duration and alpha-TRM, theta-TRM, and alpha-asymmetry-TRM. The “arrest reaction”, that is, the change in alpha and theta amplitudes from the closed to the open eyes baselines, was also tested as a predictor of subsequent performance in Pong (Cheron et al., 2016).

3.3 RESULTS

3.3.1 Behavioral data

Mean trial duration was 9012.36 ms (SD = 6803.47). An extreme outlier was identified who showed an average trial duration of 33140.07 ms, which exceeds the group’s mean by more than 3 SD hence was removed from the main analysis. After outlier removal, mean trial duration was 8180.37 ms (SD = 5141.27).

3.3.2 Theta amplitude modulation

Task engagement induced a significant enhancement of theta amplitudes at medial-parietal regions. This corresponds with the frequently observed midline theta increases and indicates the involvement of top-down control mechanisms in the task. An unpredicted decrease at posterior occipital and parietal regions was also observed. Fig. 2 displays the results for paired t-tests performed at each electrode between open eyes baseline and Pong playing, crosses indicate significant results after Bonferroni correction, and circles indicate non-corrected significant results. White color indicates amplitude increases and gray color indicates decreases.

3.3.3 Alpha amplitude modulation

Significant decreases of the alpha band were observed while playing Pong compared to the open-eyes resting baseline. These reductions were more accentuated at occipital and parietal regions as well as across the midline, but are also observable with lesser intensity at frontal and temporal sites. This implies a greater involvement of visual-processing of cortical areas in the task. Fig. 3.2 displays the results of t-tests contrasting each electrode during pong playing with itself during the open-eyes resting period.

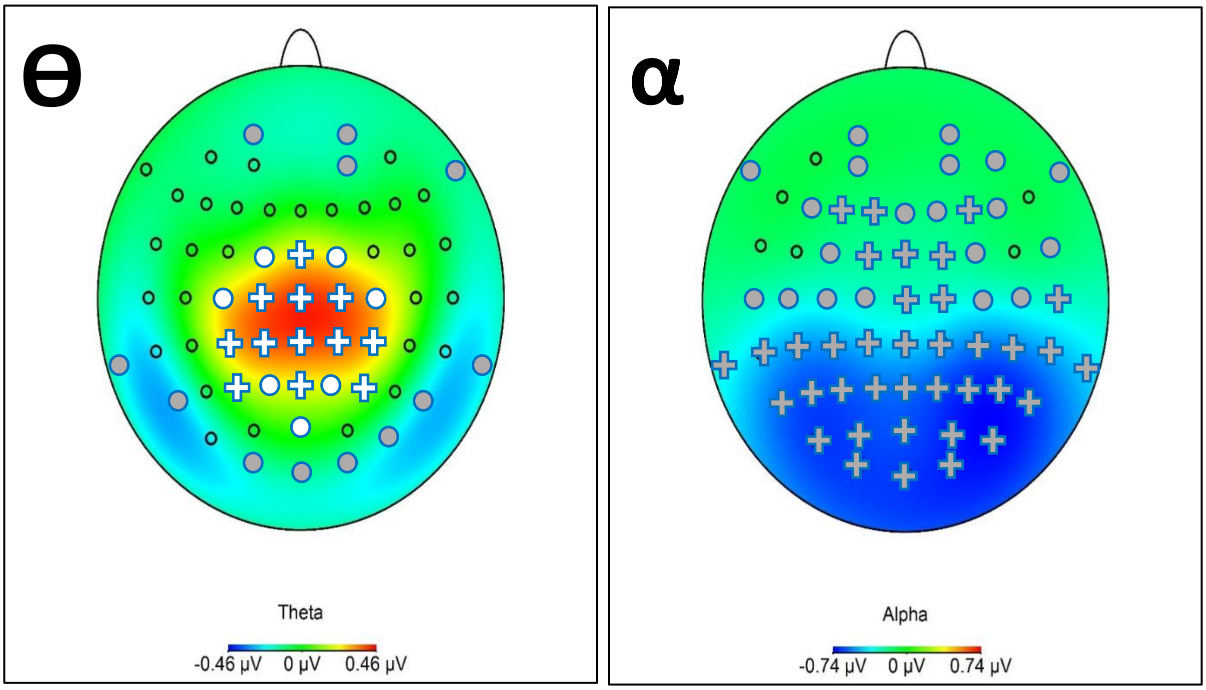

Fig 3.2. t-scores for amplitude differences between Pong-playing and open-eyes resting. For the theta (ϴ) and alpha (α) bands. The scalp maps display the subtraction of open-eyes resting from Pong-playing activity. Red color represents amplitude enhancements while playing Pong, and blue color represents amplitude decrements. Crosses (✚) indicate significance at $p < .0008$ (corrected for multiple comparisons), and circles (○) indicate significance at $p < .05$; white color indicates greater amplitude during Pong, and gray color indicating smaller amplitude.

3.3.4 Correlation of EEG modulations with performance

Task-related modulations of the theta band showed a negative correlation with trial duration in the game. Table 3.1 displays the Pearson correlation coefficient and respective significance level for all electrodes with significant correlations. As can be observed in Fig. 3.3, many of these electrodes are the same which showed significant theta enhancements, implying that with greater theta increases, performance decreased, so that trial duration was shorter. Some of the correlating locations especially at the frontal region lay outside the zone with significant enhancement, which implies that although their theta increases were smaller, they have an influence in task performance. Electrodes TP9 and PO8, which showed significant theta reductions, also show a negative correlation, which means, the greater the theta reduction in these areas, the better performance was.

Alpha amplitude reductions, despite being significant, showed no correlation with performance, similar to what has been previously reported (Cheron et al., 2016; Fairclough et al., 2005). Since most alpha reductions were statistically significant, the former suggests that while alpha suppression is necessary for task performance, it cannot discriminate performance levels.

Table 3.1.

	r(27)	*P*		*r(27)*	*p*
F5	-.368	.049	F4	-.415	.025
F1	-.390	.037	FC1	-.487	.007
F6	-.417	.024	FC2	-.526	.003
FC3	-.378	.043	FC6	-.406	.029
FC4	-.463	.011	T7	-.391	.036
C5	-.457	.013	C3	-.403	.030
C1	-.390	.036	C4	-.397	.033
C2	-.377	.044	TP9	-.427	.021
P5	-.375	.045	CP5	-.381	.041
PO8	-.376	.044	P3	-.447	.015
F3	-.397	.033	P4	-.471	.010
Fz	-.368	.050	FCz	-.538	.003

Pearson correlation between theta TRM and Pong trial duration for different electrode locations (only significant shown).

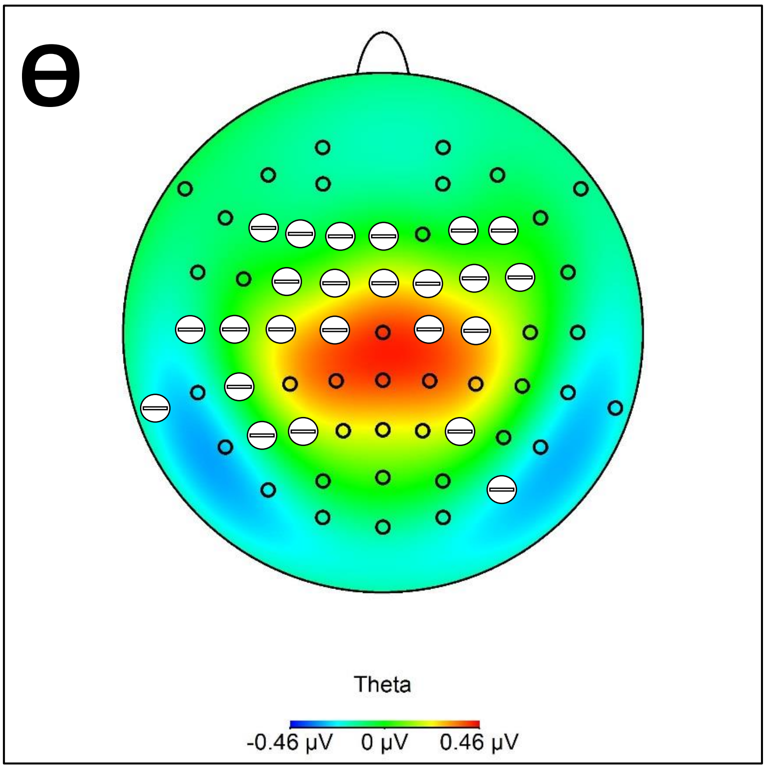

Fig 3.3. Pearson correlations between theta modulations and trial duration across all assessed electrodes. Negative correlations are represented with a minus (-) symbol. The scalp map displays the subtraction of open-eyes resting from Pong-playing theta activity. Red color represents amplitude enhancements while playing Pong, and blue color represents amplitude decrements.

3.3.5 Asymmetry modulation

The alpha asymmetry index showed significant differences between resting at electrodes PO3-PO4 (x = .009), P3-P4 (x = .018), and TP10-TP9 (0.10) with their respective levels when playing Pong (x = -.19), (x = -.018), (x = -.03). This indicates a switch from greater left sided cortical activation during baseline, to greater right sided activation when playing Pong. Fig. 3.4 displays a scalp map for alpha reductions with an adjusted scale to enhance the contrast of left and right sided activations. Homolog electrode pairs and the direction of asymmetry change are indicated. This observation is in accordance with the previous studies using Pong (Rebert & Low, 1978; Rebert et al., 1984) as well as those with dynamic and discrete visuospatial tasks, which found a greater right than left hemispheric activity at parietal and temporal areas (Janelle & Hatfield, 2008; Kerick, 2007; Kramer et al., 2007; Del Percio et al., 2009; Hatfield et al., 2004).

No correlations were found however between the alpha asymmetry index with trial duration nor was it for asymmetry modulation from baseline to activation. This suggests that while right hemispheric dominance might be necessary for task performance, this factor has lesser influence on the quality of performance. The former led to the hypotheses that right hemispheric dominance might be driven by the task in a bottom-up fashion in some individuals, while in others it might be top-down reinforced, hence driven by theta enhancements. Based on reviews by Cavanagh et al. (2014) that communication between midline theta generators and sensory cortex might serve to increase sensory gain, we performed a further correlation between theta TRM at the significant theta increase area, with alpha asymmetry modulation at the three significant pairs. Alpha asymmetry at the pair P3-P4 showed significant negative correlations with theta amplitude at electrodes C1 (*r* = -.438, *p* = .018), C2 (*r* = -.381, *p* = .041), CP3(*r* = -.413, *p* = .026), FC1 (*r* = -.388, *p* = .038), FC2 (*r* = -.429, *p* = .02) and C3 (*r* = -.398, *p* = .032), implying that greater theta amplitudes produced more rightward asymmetry between P3 and P4. Alpha asymmetry at the pair TP9-TP10 negatively correlated with theta amplitude at C1 (*r* = -.371, *p* = .047), while the pair PO3-PO4 showed no significant correlations.

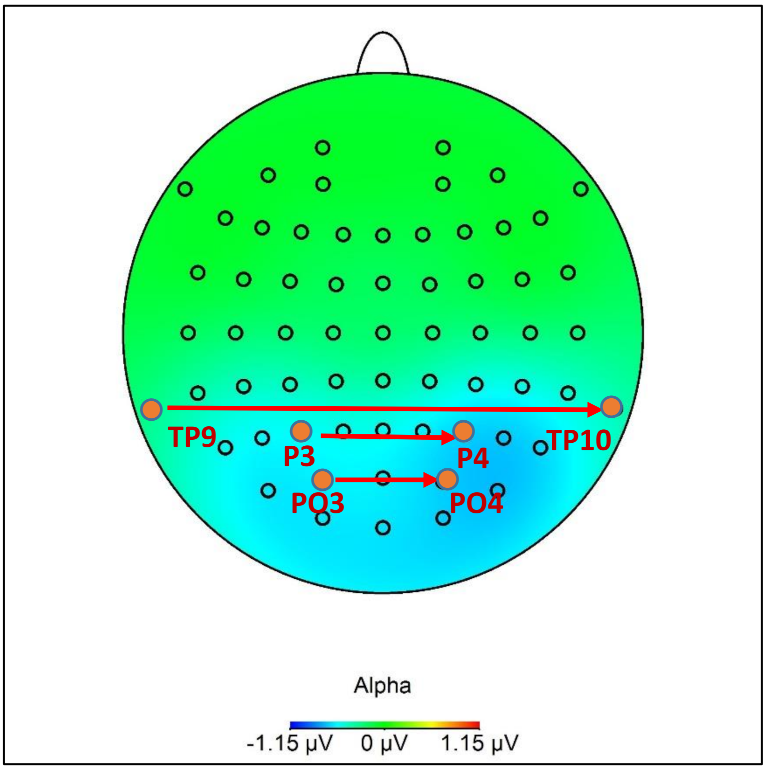

Fig 3.4. t-scores for alpha asymmetry ratio differences between Pong-playing and open-eyes resting. The scalp maps display the subtraction of open-eyes resting from Pong-playing activity, the scale has been adjusted to magnify left-right differences. The arrows indicate homolog pairs that showed significant asymmetry modulations with significance at p < .05, and the direction of the modulation.

3.3.6 Theta and alpha arrest reaction

Pearson correlation of the well-known theta and alpha reactivity to eye opening or "arrest reaction" (Cheron et al., 2016; Klimesch, 1999) with subsequent task performance produced significant results for theta (Table 3.2), and alpha (Table 3.3). Fig 3.5 displays the subtraction of closed-eyes from open-eyes activity on the scalp and indicate those electrodes that showed correlation. This coincides with previous results especially for the alpha band (Cheron et al., 2016), where a positive correlation indicates that the lesser alpha reduction after eyes opening, the better is the following task performance (Fig 3.5). Given the widespread correlations in the alpha band, we averaged the alpha arrest-reaction at all electrodes and correlated the mean with Pong performance, obtaining a medium correlation of *r(27)* = .488, *p* = .007. This correlation can be further appreciated on Fig. 3.6, smaller reductions of alpha after eye opening correlated with better subsequent task performance.

Table 3.2.

	r(27)	*p*		*r(27)*	*p*
AF3	.435	.018	C6	.381	.041
F1	.453	.014	TP7	.396	.034
F2	.397	.033	Fz	.509	.005
F6	.423	.022	F8	.429	.020
F9	.411	.027	FC1	.480	.008
FT7	.429	.020	FC6	.442	.016
FC4	.401	.031	T7	.402	.030
FT8	.372	.047			

Pearson correlation between theta arrest reaction and Pong trial duration for different electrode locations (only significant shown).

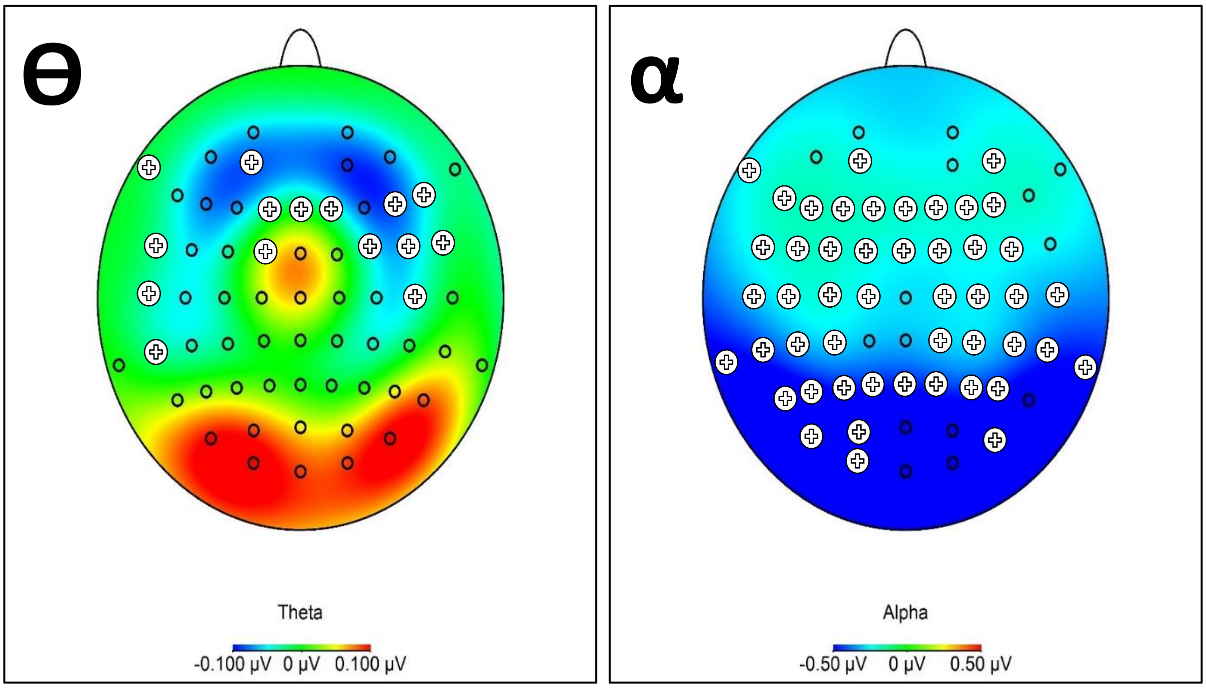

Fig 3.5. Pearson correlations between theta (Θ) and alpha (α) reactivity to eye opening and trial duration on the subsequent Pong rallies across all assessed electrodes. Positive correlations are represented with a plus (+) symbol. The scalp maps display the subtraction of closed-eyes from open-eyes resting activity. Red color represents amplitude enhancements when opening the eyes, and blue color represents amplitude decrements.

Table 3.3

	r(27)	*p*		*r(27)*	*p*
AF3	.384	.040	PO8	.393	.035
AF8	.379	.043	F7	.456	.013
F5	.372	.047	F3	.443	.016
F1	.468	.010	Fz	.375	.045
F2	.371	.047	F4	.443	.016
F6	.400	.032	FC5	.389	.037
F9	.483	.008	FC1	.431	.020
FT7	.439	.017	FC2	.425	.021
FC3	.513	.004	FC6	.410	.027
FC4	.467	.011	T7	.397	.033
C5	.405	.029	C3	.468	.010
C1	.372	.047	C4	.454	.013
C2	.493	.007	T8	.512	.005
C6	.413	.026	TP9	.423	.022
TP7	.469	.010	CP5	.481	.008
CP3	.472	.010	CP2	.472	.010
CP4	.479	.009	CP6	.430	.020
TP8	.485	.008	TP10	.451	.014
P5	.467	.011	P7	.455	.013
P1	.383	.040	P3	.416	.025
P2	.399	.032	Pz	.377	.044
P6	.412	.026	P4	.387	.038
PO7	.440	.017	O1	.397	.033
PO3	.383	.041	FCz	.372	.047

Pearson correlation between alpha arrest reaction and Pong trial duration for different electrode locations (only significant shown).

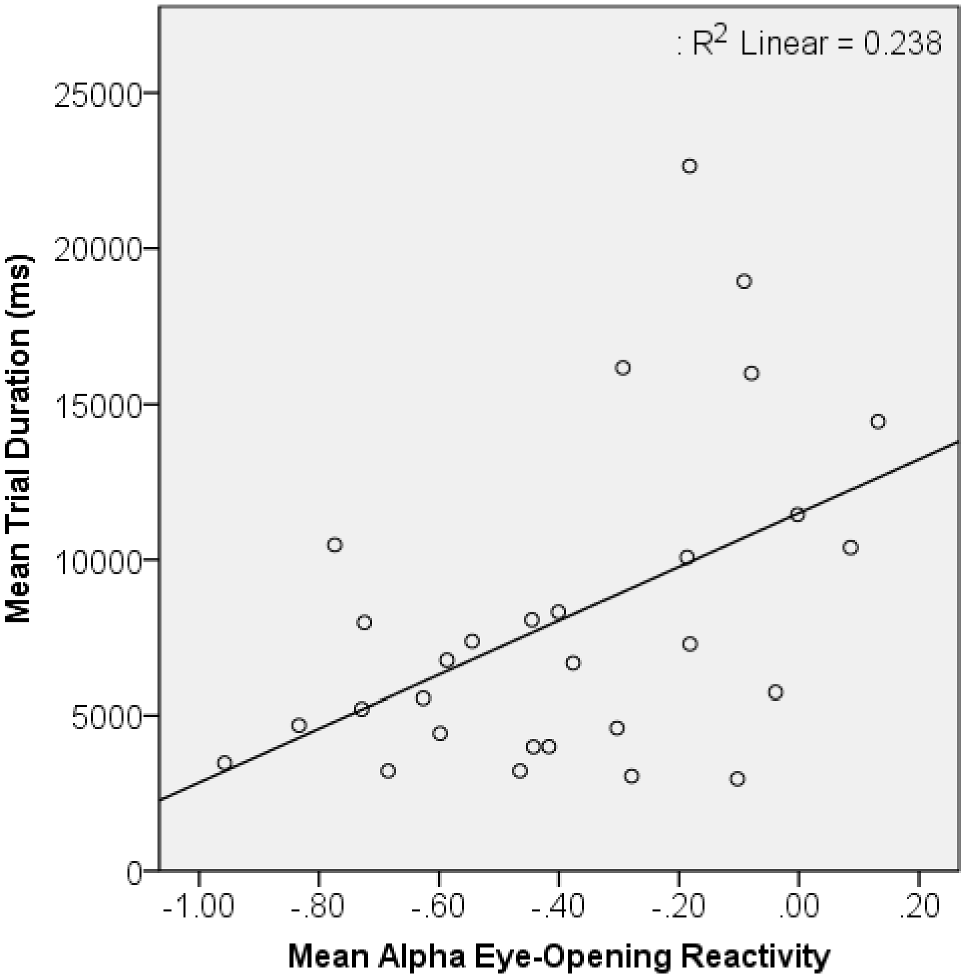

Fig 3.6. Scatter plot for the correlation between the mean alpha reactivity to eye opening or “arrest reaction” at all electrodes and the mean trial duration, used as performance criteria in the following Pong game.

3.4 DISCUSSION

In the present study we assessed the modulation of the theta and alpha band amplitude, and of the alpha asymmetry ratio during performance on the videogame “Pong” as a dynamic visuospatial task, and further correlated these modulations to performance. The well-known EEG arrest reaction to eye opening was also tested as a predictor of performance in the subsequent Pong trials. During performance, significant modulations of all indexes were observed, with an increase of theta at central and parietal cites, suppression of alpha across the whole scalp, greater over visual areas of the cortex, and a switch of the alpha asymmetry ratio from left dominance to right dominance in parietal and temporal areas. From these modulations, only the enhancement of the theta band showed a negative correlation with performance in the game. Theta enhancement also correlated negatively with right parietal alpha asymmetry modulations. We propose that theta amplitudes might be reinforcing the parietal asymmetry necessary for task performance in participants who are not yet proficient, hence theta could be acting as a sensory gain adjustment mechanism, as revised by Cavanagh et al. (2014).

The arrest reaction before engaging in the game was a predictor of performance in the following task, so that lesser suppression of the alpha band to eye opening correlated with better subsequent performance.

Widespread suppression of alpha activity during task engagement is a well-known phenomenon (Cheron et al., 2016; Borghini et al., 2014; Pineda, 2005; Fairclough et al., 2005, Klimesch, 1999; Smith, et al., 1999; Fournier et al., 1999). When comparing expert performers to novices, or the effects of training with a pre-training phase, smaller alpha suppression has consistently been observed in relation to good performance (Cheron et al., 2016; Hatfield, 2004; Del Percio et al., 2009; Smith et al., 1999). However, alpha suppression does not reach a direct correlation with performance levels on dynamic tasks, (Borghini et al., 2014; Fairclough et al., 2005; Fourier et al., 1999). Likewise, in the current study, the degree of alpha suppression along the Pong trials showed different magnitudes among participants, but these did not correlate with task trial duration as a measure of proficiency. The observation that lesser alpha suppression following eye opening correlated positively with subsequent task performance, hence leaving more room for further suppression due to task engagement (Cheron et al., 2016; Borghini et al., 2014), supports that alpha reactivity is an important factor for task performance (Doppelmayr et al., 1998; Klimesch, 1999; Klimesch et al., 2006; Jensen & Mazaheri., 2010; Hatfield et al., 2004), but it is not specific enough to discriminate performance levels.

Alpha asymmetry ratios switched from left dominance during resting, to right dominance while performing, over parietal and temporal regions. This observation is in accordance with the previous experiment using Pong (Rebert & Low, 1978) as well as with literature in both dynamic and static visuospatial tasks (Cheron et al., 2016; Del Percio et al., 2009; Janelle & Hatfield, 2008; Kramer, 2007; Hatfield et al., 2004). However, unlike Rebert & Low (1978), currently the degree of asymmetry was not related to trial duration. In this discrepancy it is important to notice two methodological differences between the studies. Rebert and Low derived alpha asymmetry by subtraction of continuous data of the right minus the left side from analogically recorded EEG, and detected the relation of alpha asymmetry and performance through data ranking and testing for differences between the ranks. On the other hand, we utilized the well-established asymmetry ratio index computed from Fourier transformed data (Davidson, 1988; Davidson, 2004; Towers & Allen, 2009), and calculated Pearson correlation. Impedance levels under 3 kΩ while recording further added reliability to our measure. In this way, it appears that rightwards hemispheric activation asymmetry is a necessary component for task performance, but is not sufficient to differentiate task proficiency within a group. Based on the former, we hypothesized that although rightwards activation asymmetry was constant among subjects, the way of its induction might have differed between proficient and non-proficient performers. In good performers it was likely induced in a bottom-up manner, driven by the high saliency of the ball's movement. Meanwhile in less proficient performers, top-down reinforcement of this asymmetry might have been necessary due to an increased need to consciously monitor task execution (Hossner &

Ehrlenspiel, 2010; Fairclough et al., 2005; Beilock and Carr, 2001; Fourier et al., 1999). Theta enhancements then would be a reflection of such top-down control (Cavanagh & Frank, 2014; Anguera et al., 2013; Sauseng et al., 2007; Inanaga, 1998).

Theta amplitude enhancements during the task showed moderate negative correlations with trial duration. This is remarkable given that other EEG measures do not commonly distinguish performance levels within a task (Cheron et al., 2016; Fairclough et al., 2005), despite being able to do so between groups or experimental conditions. A minimal degree of theta enhancement might be necessary in the task due to the necessary coordination between the visual and motor systems for performing (Cavanagh et al., 2014). However, with theta as an indicator of top-down cognitive control, the observed negative correlation indicates that those participants who required greater levels cognitive control in the task showed less proficient performance. This observation is consistent with studies of dynamic tasks which use theta as an indicator of cognitive workload (Borghini et al., 2014; Borghini et al., 2012; Beatty et al., 1974), and in contrast with self-paced discrete tasks, where event-related theta power is greater in better performers (Baumeister et al., 2008; Doppelmayr et al., 2008). This contrast likely owes to differences in the task requirements. In self-paced shooting and golf-putting, the subject needs to strongly focus attention on one point in space before executing an action, requiring strong cognitive control to do so (Baumeister et al., 2008; Doppelmayr et al., 2008; Haufler et al., 2000). Dynamic tasks on the other side, require constant monitoring of a broad visual scene, in order to execute the necessary adjustments Janelle & Hatfield, 2008; Kerick et al., 2007; Kramer, 2007; Fournier et al., 1999). In doing so, we propose that bottom-up attention guided by external stimuli is required and top-down cognitive control would only set in if this bottom-up guidance is not achieved due to factors like close monitoring of the task’s components (Hossner & Ehrlenspiel, 2010; Beilock and Carr, 2001), or distracting thoughts (Nideffer, 1992), as some participants spontaneously reported at the end of the experiment.

The above suggestion is in line with Borghini et al. (2012). Using a vigilance task while driving in a simulator, they report a greater tonic enhancement of fronto-central theta and a simultaneous decrease of parietal alpha during the dual task compared to a drive-only condition. The effect was further enhanced if the dual task was performed at night time when, due to tiredness, low frequency alpha power tends to increase despite engagement in the task, so that alpha suppression needs to be further reinforced through cognitive control (Borghini et al., 2012). This is similar to our current correlation between theta amplitudes and alpha asymmetry, with theta most likely driving parietal activation levels in less proficient players. Anguera et al (2013) also used a dual task driving game to induce transient theta enhancements in participants in a 4 week cognitive training. After training, participants improved performance, showed greater event-related theta enhancements towards each stimulus of the dual task, and showed increased connectivity between fronto-central and bilateral parietal areas, supporting the role of theta in regulating parietal activation. The reactive shooting task by Kerick et al. (2007) lies in a middle ground between dynamic and discrete visuomotor tasks, requiring constant vigilance before target appearance, and focused attention once the target appears. Theta was only measured around target onsets, however, when a secondary arithmetic task was included, target-related theta enhancements delayed their onset. This implies that the imposition of cognitive workload, related to tonic theta enhancements, delayed the onset of additional transient cognitive control Fourier et al (1999) and affected performance in this dynamic task Kerick et al., (2007).

The central-parietal location of our theta enhancement can be attributed to the visual nature of the task. This distribution reflects the involvement of parietal association areas in thoroughly analyzing visual stimuli (cf. Kerick et al., 2007) in the Pong task, most likely in order to predict the ball's trajectory. Tasks with elevated visual requirements have been reported to have a posterior locus for theta modulations (Fourier et al, 1999; Fairclough et al., 2005; Kerick et al., 2007). For example, in the reactive shooting task by Kerick et al. (2007) where friendly and enemy targets had to be quickly identified, theta enhancements were also observed over central-parietal rather than frontal-central areas.

In the current study differences in theta enhancements are due to participant skill and not due to external distractors, greater task difficulty, or secondary tasks. It is difficult to point to a single factor that contributed difficulty for each participant. For instance, some reported the need to inhibit an impulse to mirror the ball's movements with the paddles, others reported distracting self-talk, found it difficult to predict the ball's trajectory, or struggled to coordinate the two paddles. Generally however, all of these factors imply a conscious monitoring of the task's components (Hossner & Ehrlenspiel, 2010; Beilock and Carr, 2001) and can be said to bring additional cortical activation, which competes with the parietal regions (Hatfield, 2004; Kobayashi et al., 2004; Hilgetag et al., 1999; Kapur, 1996) and requires greater inter-regional coordination. Central theta is thought to participate in the coordination of disperse cortical areas facilitating information exchange between them (Cavanagh et al., 2014; Klimesch et al., 2006). Its origin is traced to be at the mid-cingulate cortex (Cavanagh et al., 2014), which is a strategic region for the transfer of information due to its central location.

Finally, we observed an unpredicted decrease of theta at far posterior parietal and occipital locations, and greater decrements correlated with better performance. This observation, nonetheless coincides with a study by Beatty et al. (1974) where radar operators who learned to decrease theta levels at this location, became more efficient in the task. Reduced levels of posterior theta are independent of central theta, and have been related to arousal processes (Beatty et al., 1974; Lin et al., 2010), so that it is likely that the current participants enhanced alertness during task performance.

3.5 CONCLUSIONS

From the currently assessed EEG measures during the Pong task, theta modulation was the most reliable indicator of the task proficiency, with greater levels of theta enhancement correlating with worst levels of performance. This implies that, in contrast to discrete tasks, greater levels of cognitive control were detrimental in dynamic task performance, and supports the idea that a greater bottom-up rather than top-down guidance of attention facilitates performance in skilled dynamic tasks is helpful for better performance. The use of central theta is therefore recommended in further studies which analyze dynamic tasks such as sport performance to assess the effects of learning, stress or task difficulty. In addition, the Pong game, proved useful as a dynamic task in the laboratory. It can be profitably used to analyze the mechanisms of cognitive control during fluid performance, as task variables can be easily manipulated to allow for cognitive inference.

As in previous studies, alpha amplitude significantly decreased during the task, and its asymmetry ratio showed greater right-sided activation, but neither of these modulations achieved a correlation with performance. However, alpha reactivity to eye opening was moderately predictive of subsequent performance in this complex task, with small alpha reductions commonly anticipating better performance. Since smaller eye-opening alpha suppression implies greater room for further suppression due to task performance, we conclude that although alpha suppression is essential for performance, it is not sensitive enough to differentiate performance levels.

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Chapter 4

Stress induction improved performance and reduced theta amplitude

Stress induction improved performance and reduced theta amplitude

4.1 OVERVIEW OF THE CHAPTER

On the previous chapter, the EEG modulations when engaging in the videogame “Pong” as a dynamic visuospatial task were presented. The alpha band showed the expected task-related suppression, more accentuated on the right parietal and temporal sites, replicating previous research (Rebert & Low, 1978, Cheron et al., 2016; Del Percio et al., 2009; Janelle & Hatfield, 2008; Kramer, 2007; Hatfield et al., 2004). The theta band showed significant increases over the midline also replicating previous research (Rebert et al., 1984), but most importantly, this increase correlated negatively with the participants’ performance level. The main intention of the study was, however, to test the effects of dynamic handgrip on the prevention of visuomotor skill failure in a following stress-induction block.

In the current chapter, the results of the stress-induction block are presented. The same participants as in the previous chapter took participation. They were divided into three groups with 10 participants each, one group with left dynamic handgrip before stress performance, one with right, and one with no handgrip. It was hypothesized that stress induction would deteriorate performance in the right-handgrip and no-handgrip groups, while the left-handgrip group would be resistant to the effects of stress due to the induction of greater alpha levels post-contractions (Cross-Villasana et al., 2015).

Although all groups reported a subjective increase in stress, all groups improved performance under the stress block and stress levels were not correlated to performance. Therefore, the effects of dynamic handgrip on the task could not be explored. However, task-related theta amplitude was diminished during stress compared to the stress-free block, and it no longer correlated with performance. Given that performance during the stress block was superior, this supports the notion that greater theta levels hinder performance in this dynamic task. Moreover, the individual participant’s patterns of theta activation over the scalp variated from the pattern seen in the grand average to various degrees, but were remarkably consistent on each subject between the two experimental blocks (see chapter Annex). Such consistency supports that these particular individual patterns do not result from noise in the recordings, they may likely reflect the different strategies followed by the participants in the game. As with the stress-free block, in the stress block the alpha arrest reaction continued to correlate with subsequent performance

4.2 MATERIALS AND METHODS

The participants, task and apparatus were the same as in the previous chapter. For behavioral analysis, performance outliers were not excluded, since the main factor is change in performance between blocks instead of absolute performance. At the beginning of the training session before the experiment, participants were informed that in the second block, the effects of stress were tested, in which stress would be induced through a performance criterion they would need to match, and that would be communicated to them before that stress block. As a cover story, it was also explained to them that during the stress block, facial expression was going to be analyzed, therefore a video-camera was going to record their face. In reality however, the use of the camera was in itself intended as a stress inductor (Jackson et al., 2006). Privacy and confidentiality of the data were assured to all participants.

After completing the stress-free block, two questions with a Likert scale of seven points were presented to the participant: “How important was it for you to have good performance on the task?” and “How much did you feel under pressure during the test?” Afterwards, a break ensued where participants were reminded about the inclusion of the camera and informed that the performance criterion they needed to meet in the following stress block was their own average during the stress-free block. In order to facilitate skill-failure, they were also reminded of the verbal cues given during the training “always anticipate the ball, keep the paddle in the middle and to try to hit the ball with the center of the paddle”, so that these cues would interfere with automatic task performance (Beckmann et al., 2013). Before engaging in the stress block, the handgrip manipulation was introduced to the participants in the left and right handgrip groups, as a stress-coping technique. All participants except those in the no-handgrip group, performed dynamic handgrip with either left or right hand depending on the group, as in Cross-Villasana et al., (2015), that is, squeezing a rubber ball completely with all fingers for 45 seconds at a pace of approximately 2 per second. After finishing the manipulation, participants released the ball on a base placed on their right or left, and started the game with a spacebar press. The block consisted of 15 trials. At the end of the game, the comparison of their stress-free and under-stress average were presented. If the stress average did not surpass the stress-free average, it was displayed with red letters. The participants responded the Likert items again regarding their experience during the stress block.

4.3 BEHAVIORAL RESULTS

4.3.1 Task performance

On the stress-free block, the left-handgrip group incidentally showed the poorest performance (*M* = 6757.53 ms, *SD* = 3223.29). When compared to the right-handgrip group which had the highest performance (*M* = 10955.34 ms, *SD* = 6708.08), the difference trended towards statistical significance, *t*(18) = -1.78, *p* = .09. The performance of the neutral group (*M* = 9324.22 ms, *SD* = 9154.66) showed no significant differences with either of the other groups. During the stress block, all groups improved but between-groups comparisons showed the same pattern (Fig 4.1-A), so that the left-handgrip group still showed the worst performance (*M* = 8226.87 ms, *SD* = 3629.15), reaching a marginally significant difference with the right-handgrip group (*M* = 12616.79 ms, *SD* = 6408.95), *t*(18) = -1.86, *p* = .07, which showed the best performance. The no-handgrip group showed no significant differences with the left or right handgrip groups. Regarding within-group performance in the two blocks, only the left-handgrip group showed a marginally significant difference *t*(9) = -2.23, p = .053.

When contrasting the improvement from the stress-free to the stress block for the left-handgrip (*M* = 1469.33 ms, *SD* = 2087.84), right-handgrip (*M* = 1661.45 ms, *SD* = 2999.18), and no-handgrip

(*M* = 2068.00 ms, *SD* = 4011.67), no significant differences were found (Fig 4.1-A). There were also no differences in the number of trials in which the criterion was not reached between the left (*M* = 7.5 ms, *SD* = 1.43), right (*M* = 8.1 ms, *SD* = 1.00) or no-handgrip group (*M* = 8.1 ms, *SD* = 3.11), so that all teams surpassed the criterion in around half of the trials. Of the participants whose stress performance average did not surpass that of the stress-free block, two were on the left-handgrip group, one in the right-handgrip and four at the no-handgrip group.

4.3.2 Self-reported stress

Overall, stress levels were low to mild, between 3 and 5 in a 7 scale Likert item. The left-handgrip group showed the smallest difference in self-reported stress (*M* = 0.3, *SD* = 1.34) between conditions (Fig 4.1-B), with a level of (*M* = 4.3, *SD* = 1.70) during the stress-free block, and (*M* = 4.6, *SD* = 1.65) under stress, which was not statistically significant. The right-handgrip group showed a significant increase (*M* = 1.0 , *SD* = 1.34) in self-reported stress on the stress-block (*M* = 3.9, *SD* = 1.29) compared with the stress-free block (*M* = 2.9, *SD* = 1.29), *t*(9) = -4.74, *p* = .001. The no-handgrip group also showed a significant increase (*M* = 1.4, *SD* = 1.17) of subjective stress during stress (*M* = 5.20, *SD* = 1.31) compared to the stress-free block (*M* = 3.80, *SD* = 1.92), *t*(9) = -3.77, *p* = .004). This observation suggests that left-handgrip was effective in reducing task-related stress, however performance levels also improved under the stress block for groups which increased their stress levels.

Higher performance under the stress condition suggests that stress could have boosted rather than deteriorated performance, however no positive correlations were observed between self-reported stress and trial duration. Instead, a negative correlation was observed in the left-handgrip group during the stress-free block *r*(8) = -.68, *p* = .03, and two negative correlations trending towards significance in the right-handgrip group on the stress-free *r*(8) = -.57, *p* = .09, and the stress block *r*(8) = -.60, *p* = .07. Therefore the data does not support that higher levels of stress could have improved performance levels.

4.3.3 Self-reported importance of performance

All groups reported giving high levels of importance to their performance levels on the stress-free block, above 4 in a 7 scale Likert item. These further increased during the stress block. On the left-handgrip group, this increment was significant, with greater importance given on the stress block (*M* = 6.4, *SD* = .84) compared to the stress-free block (*M* = 5.9, *SD* = .99), *t*(9) = -3.0, *p* = .02. The right-handgrip group also showed a significant increase in importance given to performance during the stress block (*M* = 6.2, *SD* = .79) compared to the stress-free block (*M* = 5.7, *SD* = 1.06), *t*(9) = -3.0, *p* = .02. The no-handgrip group showed no significant difference between the stress (*M* = 6.3, *SD* = 1.05) and stress-free blocks (*M* = 6.0, *SD* = .82). These results indicate that all participants in all groups devoted enough effort in the task, and that stress induction did not decrease it.

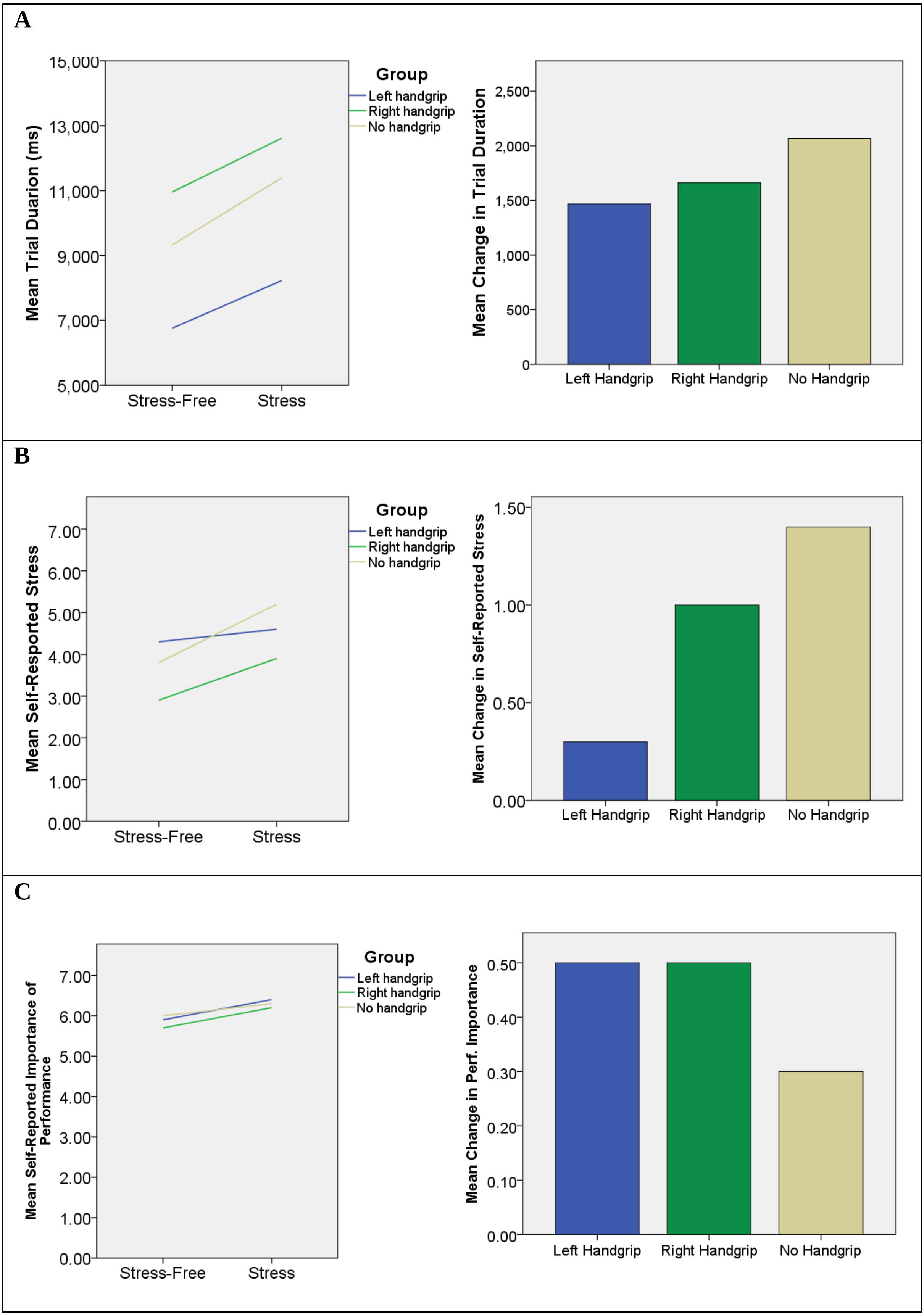

Fig 4.1. Line and bar plots showing respectively the levels of the assessed parameters and their degree of change between the stress-free and stress blocks. A) For trial duration. B) For self-reported-stress. C) For importance given to performance.

4.4 ELECTROPHYSIOLOGICAL RESULTS

Considering the greater performance observed during the stress-induction block, differences in the pertinent task-related EEG modulations between the blocks were explored. Since the effects of dynamic handgrip are no longer explored in this regard, the participants were no longer divided in groups for analysis. To homologize with the analysis made for the stress-free block, the performance outlier was excluded from the analysis.

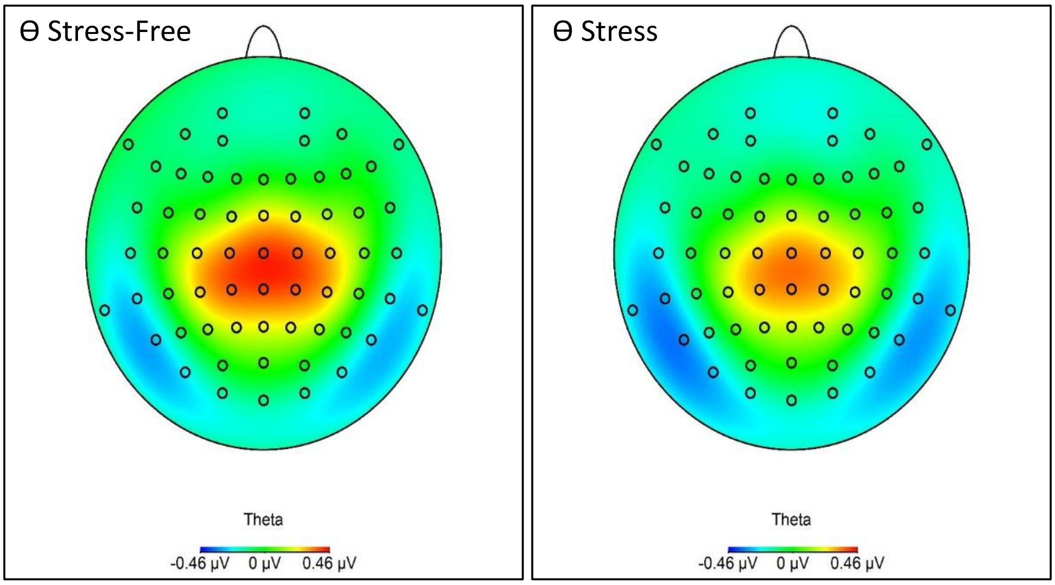

Fig 4.2. Scalp maps of the task-related modulations in the theta (ϴ) band obtained by subtracting amplitude values of the open-eyes baseline from those during the stress-free and stress blocks. Red color represents amplitude enhancements and blue color represents amplitude decrements.

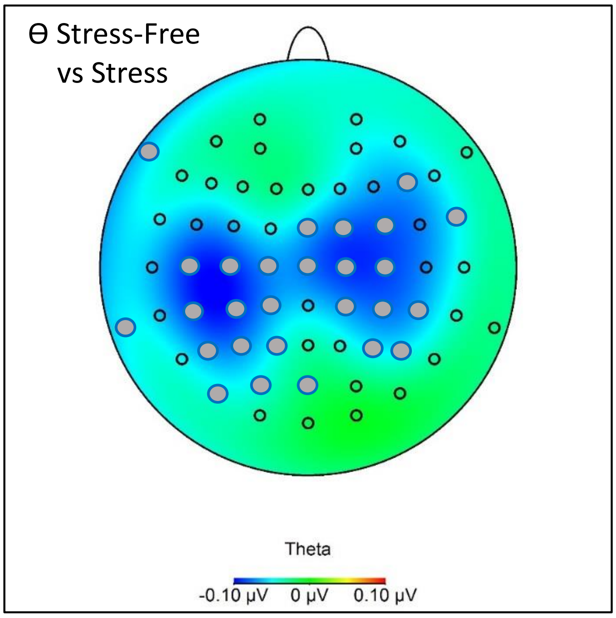

Fig 4.3. t-scores for amplitude differences between the stress-free and the stress block for the theta (ϴ) band. The scalp maps display the subtraction of the stress-free from the stress block activity. Blue color represents smaller amplitude for the stress block. Circles (○) indicate significance at p < .05.

4.4.1 Theta amplitude modulation

Theta amplitudes during the stress block, showed a smaller task-related increment over central regions and a greater decrement over occipital and posterior parietal regions than the stress-free block (Fig 4.2). Pair-wise t-tests revealed significant differences between the two blocks at numerous electrodes (Fig 4.3). Since both conditions produce modulations in the same direction, Bonferroni correction was not considered. These modulations suggest that participants decreased top-down control and enhanced arousal when performing in the stress-block. Unlike the stress-free block, the stress block, showed no correlation of theta amplitudes with performance, due to the better performance and lower of theta level.

4.4.2 Alpha amplitude modulation

Alpha amplitudes during the stress block showed the same pattern of reductions than the stress-free block with slightly greater intensity (Fig 4.4). Pair-wise t-tests of task-related suppression between the two blocks revealed significantly greater suppression during the stress block mainly at left parietal regions (Fig 4.5). Unlike in the stress-free block, in the stress block alpha suppression showed low positive correlation with performance at electrodes P5, *r*(27) = .38, *p* = .04*;* PO3, *r*(27) = .40, *p* = .03; O1, *r*(27) = .38, *p* = .04; and O2, *r*(27) = 38, *p* = .05. Given that alpha suppression is a negative number, this positive correlation implies that the lesser alpha suppression (less cortical activation) in these electrodes, mostly on the left parietal region improved performance.

When analyzing alpha amplitude, the results of correlation and those of between block comparisons appear to contradict each other. The stress block showed better performance yet had greater left sided mean alpha suppression than the stress-free block. At the same time, correlation analysis within the stress block shows that the lesser alpha suppression in the same region is related to better performance. Case inspection revealed that the few participants who decreased performance on the stress block tended to have a marked left sided alpha suppression, hence contributing to the correlation, and the results of the comparative scalp map with the stress-free block (Fig 4.5). To confirm the role of activation asymmetry in performance, the more precise alpha asymmetry ratio was analyzed.

4.4.3 Alpha asymmetry modulation

In comparison with the stress-free block, the stress block showed significant modulation of the alpha asymmetry ratio of only one electrode pair (Fig 4.6). The asymmetry index showed that the pair PO3-PO4 significantly switched from leftward (*M* = 0.1, *SD* = .04) activation dominance in baseline, to rightward (*M* = -0.1, *SD* = .04), *t*(28) = 2.08, *p* = .047 activation dominance during the stress-block. Pair TP9-TP10 showed a marginally significant switch in the same direction from leftward (*M* = 0.1, *SD* = .07) to rightward (*M* = -0.2, *SD* = .06) activation dominance, *t*(28) = 2.08, *p* = .053. Like in the stress-free block, Pearson correlation analysis revealed no correlations between asymmetry levels and task performance during the stress-block.

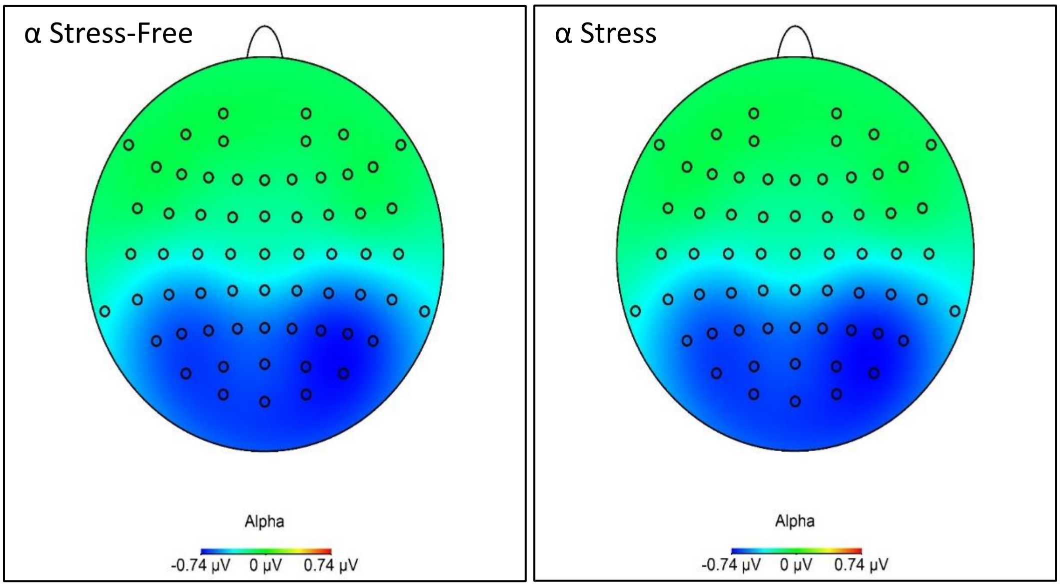

Fig 4.4. Scalp maps of the task-related modulations in the alpha (α) band obtained by subtracting amplitude values of the open-eyes baseline from those during the stress-free and stress blocks. Blue color represents amplitude decrements.

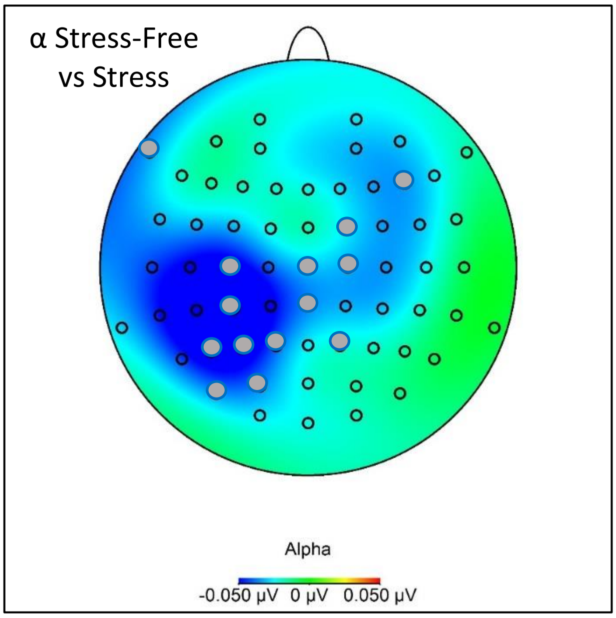

Fig 4.5. t-scores for amplitude differences between the stress-free and the stress block for the alpha (α) band. The scalp maps display the subtraction of the stress-free from the stress block activity. Blue color represents smaller amplitude for the stress block. Circles (○) indicate significance at $p < .05$.

When comparing the alpha asymmetry ratios of each block to each other, electrode pair PO3-PO4 showed a significant difference, with greater rightwards activation asymmetry for the stress-free ($M = -0.2$, $SD = .05$) than for the stress block ($M = -0.1$, $SD = .04$), $t(28) = 2.07$, $p = .048$. As can be observed in Fig. 4.6 the greater overall alpha suppression during the stress block, eliminated the statistical difference between pairs P3-P4 and TP9-TP10, despite suppression still being asymmetric.

Analysis of task related alpha modulation and asymmetry ratio suggest that although alpha suppression, greater on right posterior regions, is a necessary component of performance, it is an unstable marker of performance levels. The ratio of alpha suppression at each hemisphere is affected by the overall levels of suppression, hence making it difficult to obtain stable correlations with performance, or consistent differences between blocks.

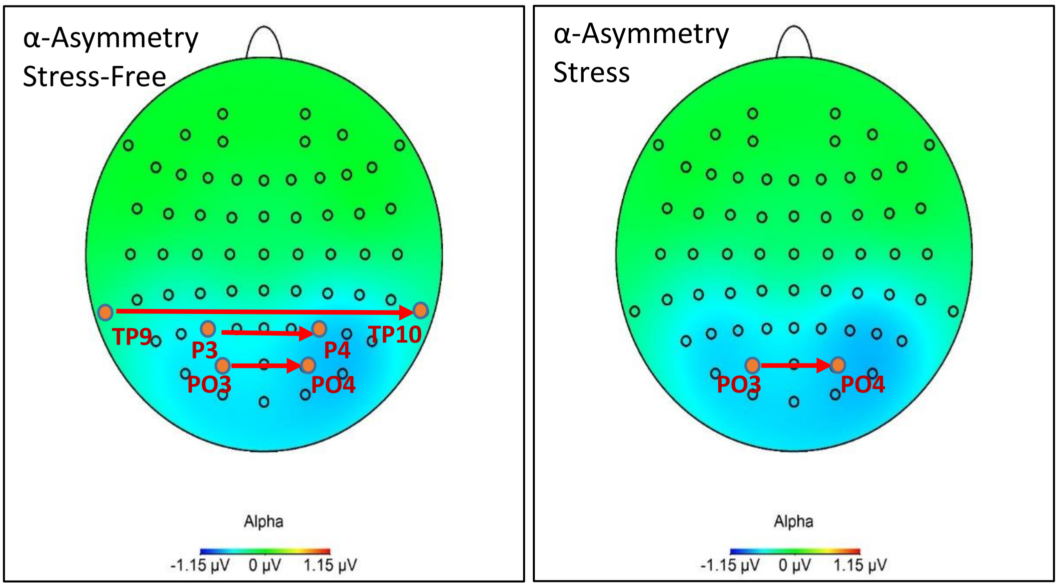

Fig 4.6. Significant alpha asymmetry ratio modulations obtained from t-scores between open-eyes resting and Pong playing during the stress-free and the stress blocks. The scalp maps display the subtraction of open-eyes resting from each of the Pong-playing blocks. The scale has been adjusted to magnify left-right differences. Homolog electrode pairs that showed significant asymmetry modulations are highlighted and joined by arrows that indicate the direction of the modulation.

4.4.4 Theta and alpha arrest reaction

The arrest reaction to eye opening showed medium positive correlations between performance during the stress block with the theta (Table 4.1) and especially with the alpha band (Table 4.2). In this way, like in the stress-free block, lesser suppression of alpha after opening the eyes was related to better performance in the stress block. In the alpha band, the magnitude of the correlations in the stress-block was greater than it was for the stress-free block, given that the stress block produced greater alpha suppression when playing Pong. This confirms that the levels of resting alpha amplitude are predictive of subsequent task performance (Doppelmayr et al., 1998; Klimesch, 1999; Jensen & Mazaheri., 2010; Hatfield et al., 2004) because smaller alpha suppression after opening the eyes, leaves greater room for further suppression due to task engagement (Cheron et al., 2016). The role of the theta arrest reaction is less certain, as it is not uniform across the scalp (Fig 4.7) and has not been previously explored, but overall, greater upregulations and downregulations in their corresponding regions, correlated with greater performance.

Table 4.1.

	r(27)	*P*		*r(27)*	*p*
AF7	.398	.033	FP1	.385	.039
AF3	.456	.013	FP2	.375	.045
AF8	.429	.020	F7	.404	.030
F1	.460	.012	F3	.398	.032
F2	.406	.029	Fz	.442	.016
F6	.535	.003	F4	.389	.037
F9	.463	.011	F8	.514	.004
FT7	.373	.046	FC1	.434	.019
FC4	.482	.008	FC2	.420	.023
FT8	.407	.029	FC6	.505	.005
F10	.377	.044	C4	.396	.034
C6	.433	.019	CP6	.369	.049
TP7	.416	.025	P7	.390	.036

Pearson correlation between theta arrest-reaction and Pong trial duration during the stress-block for different electrode locations (only significant shown).

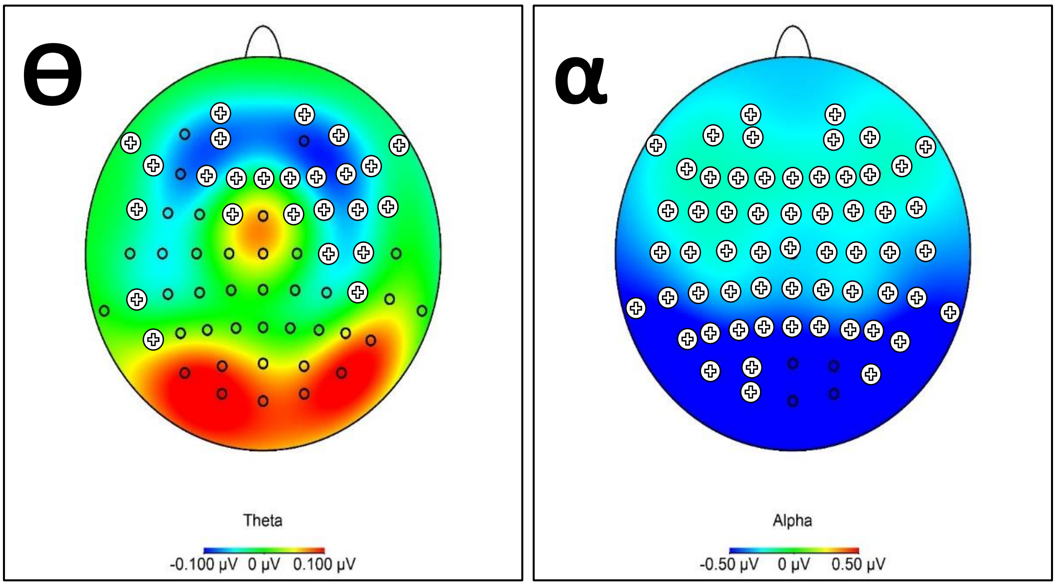

Fig 4.7. Pearson correlations between theta (Θ) and alpha (α) reactivity to eye opening and trial duration on the subsequent Pong rallies in the stress block across all assessed electrodes. Positive correlations are represented with a plus (+) symbol. The scalp maps display the subtraction of closed-eyes from open-eyes resting activity. Red color represents amplitude enhancements when opening the eyes, and blue color represents amplitude decrements.

Table 4.2.

	r(27)	*P*		*r(27)*	*p*
AF7	.420	.023	FP1	.442	.016
AF3	.455	.013	FP2	.407	.028
AF4	.400	.032	F7	.537	.003
AF8	.462	.012	F3	.505	.005
F5	.481	.008	Fz	.494	.006
F1	.574	.001	F4	.554	.002
F2	.490	.007	F8	.481	.008
F6	.531	.003	FC5	.430	.020
F9	.566	.001	FC1	.521	.004
FT7	.508	.005	FC2	.553	.002
FC3	.524	.004	FC6	.522	.004
FC4	.608	<.001	T7	.447	.015
FT8	.449	.015	C3	.485	.008
F10	.471	.010	Cz	.468	.010
C5	.479	.009	C4	.513	.004
C1	.481	.008	T8	.554	.002
C2	.561	.002	TP9	.509	.005
C6	.517	.004	CP5	.466	.011
TP7	.541	.002	CP1	.391	.036
CP3	.460	.012	CP2	.476	.009
CPz	.403	.030	CP6	.407	.028
CP4	.415	.025	TP10	.463	.011
TP8	.488	.007	P7	.538	.003
P5	.494	.006	P3	.432	.019
P1	.461	.012	Pz	.471	.010
P2	.449	.015	P4	.384	.040
P6	.446	.015	P8	.435	.018
PO7	.513	.004	O1	.463	.012
PO3	.467	.011	FCz	.503	.005
PO8	.435	.018			

Pearson correlation between alpha arrest-reaction and Pong trial duration during the stress-block for different electrode locations (only significant shown).

4.5 DISCUSSION

All groups showed an increase in self-reported stress on the stress block, implying that the stress condition did increase subjective stress levels, although stress levels remained moderate. However, performance during the stress block was also superior to the stress-free block in all groups. In this way, the preventive effects of dynamic handgrip for performance under stress could not be tested. A lack of correlation between subjective stress and performance levels suggests that it was not due to greater subjective stress that performance improved. Participants reported giving sufficient importance to their performance on each block, so that this may not be a confounding factor. It is likely that the requirement for the participants to improve their own baseline performance served as a goal setting (Locke & Latham; 2002) which facilitated attention towards the task despite of the presence of a video camera, a known stressor element (Jackson et al., 2006). Therefore, alternative stress induction strategies in the laboratory need to be developed in order to test the effects of stress on performance, and its prevention.

During the stress block, theta amplitudes decreased compared to the stress-free block. Given the better performance in the stress block, lower levels of theta support that less cognitive control in dynamic visuospatial tasks is helpful for performance. This complements the negative correlation of theta with performance during the stress-free block. In the stress block this correlation was no longer found, due to most participants improving performance and decreasing theta compared to the stress-free block, hence decreasing variability on the data. Altogether, the analysis provides a consistent picture where greater central theta negatively affects performance, so that greater top-down cognitive control hinders performance in dynamic visuospatial tasks like Pong.

Alpha amplitudes showed a greater decrease under the stress block, reaching significance at various locations, implying greater cortical activation under the stress block. Paradoxically the most intense difference between the blocks was on the left parietal instead of the right parietal area. Considering the better performance on the stress block, this observation contrasts with the persistent finding that visuospatial tasks require dominant right parietal activation (Cheron et al., 2016; Del Percio et al., 2009; Janelle & Hatfield, 2008; Kramer, 2007; Hatfield et al., 2004; Rebert & Low, 1978). The contrast was due to the few participants who worsened their performance on the stress block, who tended to have higher left parietal alpha suppression, hence correlation analysis showed a weak tendency where lesser left parietal alpha suppression lead to better performance. As a result of increased overall cortical activation, as reflected by alpha suppression, the level of activation asymmetry between the hemispheres was reduced on the stress block, and became significant only at one pair of homolog electrodes. The alpha asymmetry ratio did not show correlation with performance in either block. Altogether, although task-related alpha modulations and their asymmetry reflect necessary processes for performing this visuospatial task, they were unstable markers of proficiency.

Despite the former, the importance of alpha in performance is highlighted by the correlation between the alpha arrest-reaction to eye opening and subsequent performance. The correlation in the stress block was greater than that during the stress-free block, due to the stress block showing greater alpha suppression while performing. This supports that higher alpha levels at rest benefit subsequent performance, even in a complex task as Pong, which is not specially geared at assessing a single cognitive system.

4.6 CONCLUSIONS

The findings support the EEG theta band over the alpha band and its asymmetry as a more robust marker of performance proficiency. In dynamic tasks, alpha is more vulnerable to the multiple processes occurring while performing such as constant redirections of attention, and requires a greater control of experimental conditions which is perhaps not achievable in dynamic tasks. Theta represents a single process of cognitive control, which is proposed to mediate between multiple cortical regions, but which is generally observable on the midline on the scalp despite having between-subject variations (see Annex). In this way it is more resistant to factors like the aforementioned redirection of attention. It can be said that as the performers achieve greater cognitive economy (Hatfield et al., 2004; Haufler, 2000), and less coordination is needed between cortical regions, theta would diminish its levels as cognitive control becomes less necessary (Cavanagh & Frank, 2014; Sauseng et al., 2007). Hence theta can be a robust marker to use in studies that analyze the effects of learning, stress or difficulty on dynamic tasks.

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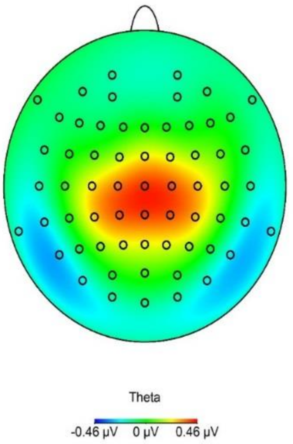
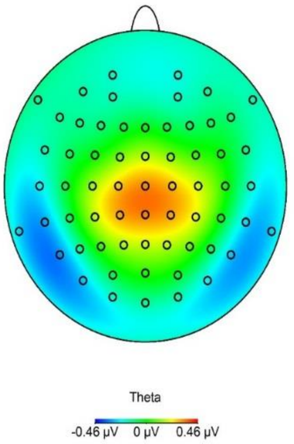
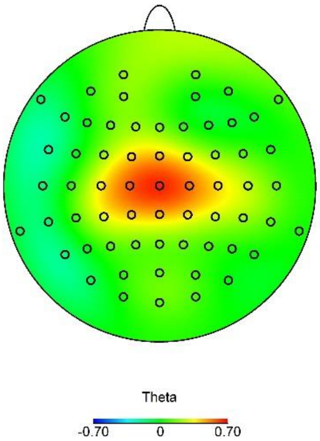
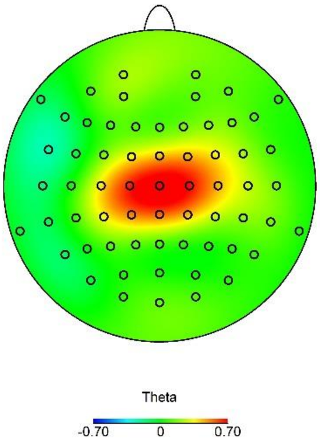
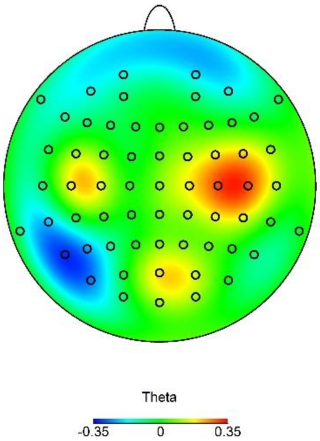
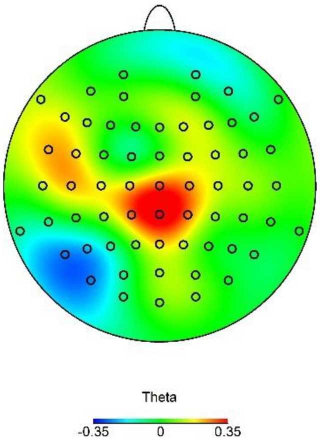
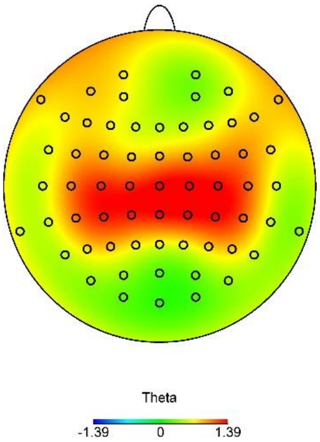
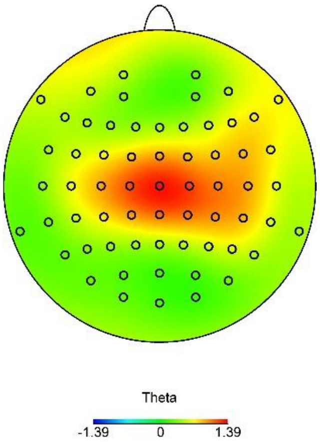
ANNEX: Persistent patterns of theta activation within subjects.

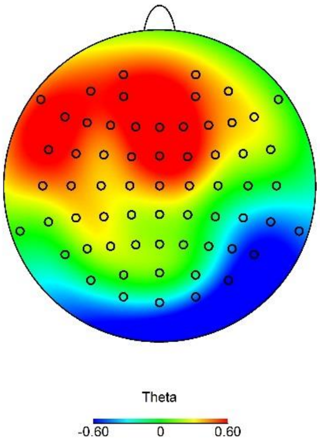
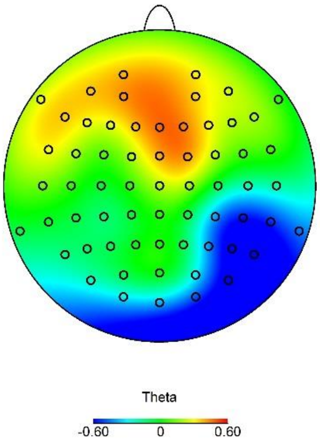
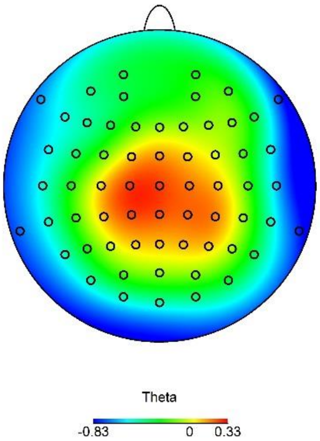
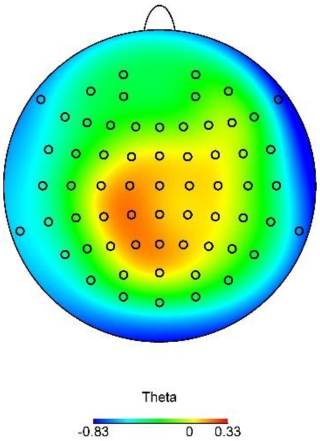
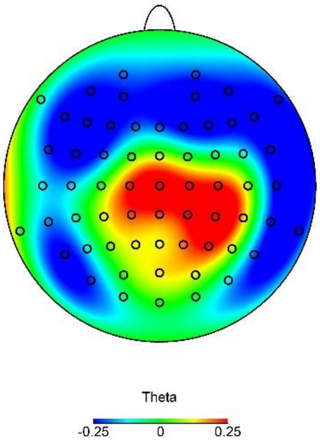
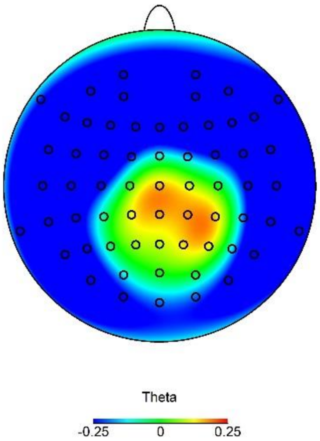
Theta task-related modulations showed a consistent pattern in the average of the stress-free and the stress block only with different intensity. This consisted of a central enhancement and posterior decrease in both blocks with smaller central enhancement and greater posterior decrease during stress. Despite of this average picture, examination of each individual participant revealed variations from the average in different degrees. However, the individual patterns of theta modulations between the two blocks were also remarkably consistent for most participants, varying only in the strength of the modulations. Scalp maps of all participants, are displayed below, with excluded participants in the end. In these maps, it is also noticeable how in most cases, theta reductions coincide with better performance.

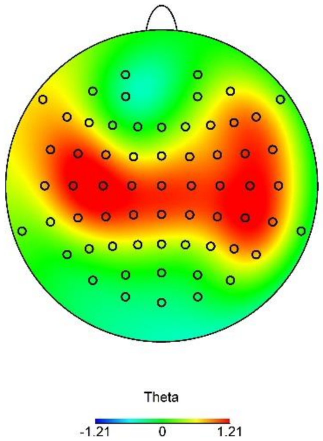
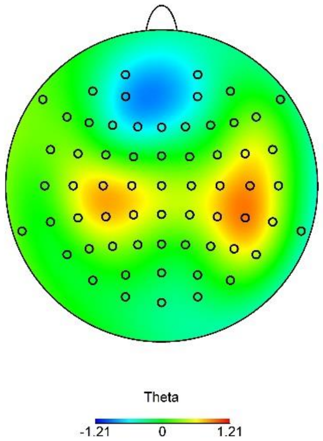
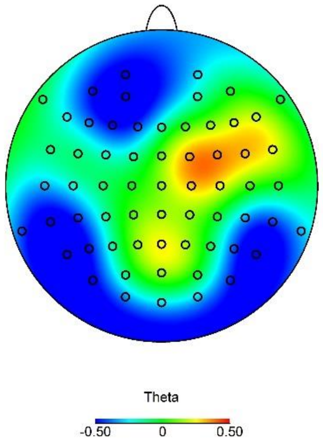
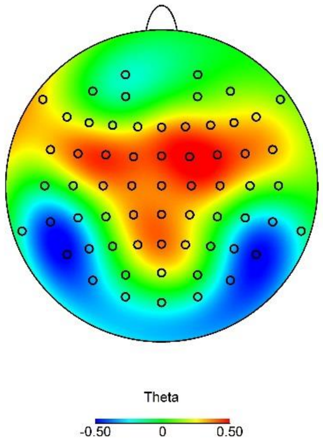
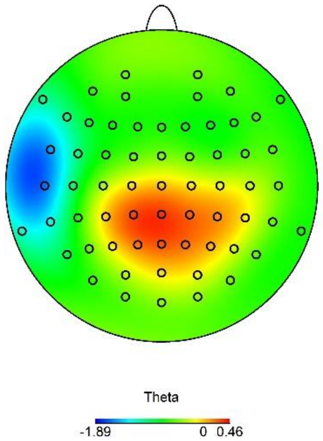
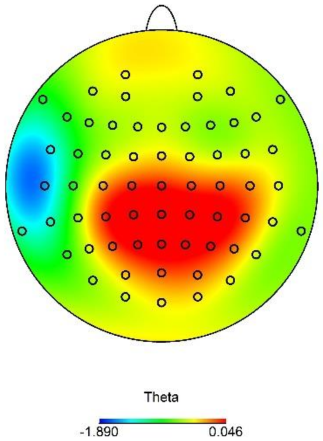
Such consistency in almost all participants, supports that these individual patterns do not result from noise in the recordings. These pattern might rather reflect the individual strategy followed by the participants in trying to solve the task, or the kind of difficulty they faced while performing, which called for close monitoring, and therefore, cognitive control. The activation patterns share a midline component, presumably reflecting the action of the mid-cingulate cortex as the main source of theta (Cavanagh et al., 2014; Klimesch, 1999), but from there travel to different regions of the scalp on each participant, so that only the medial component remains in the grand average.

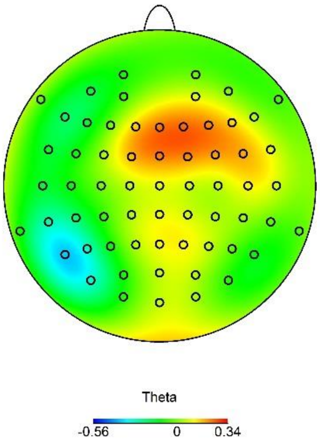
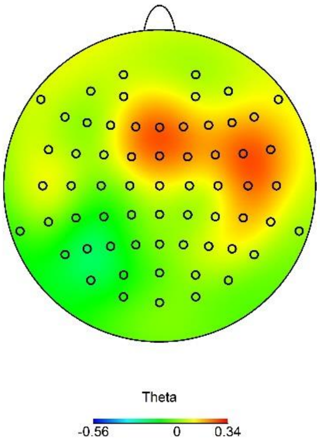
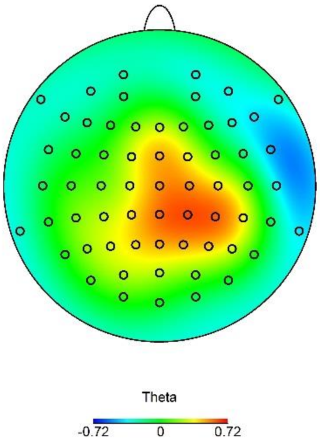
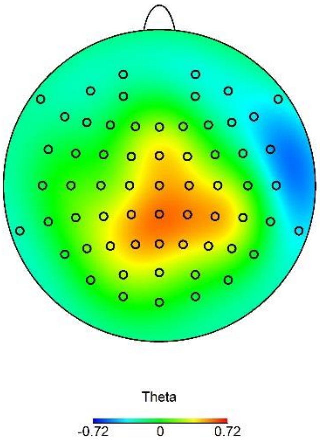
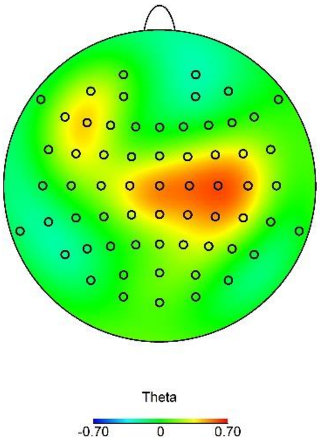
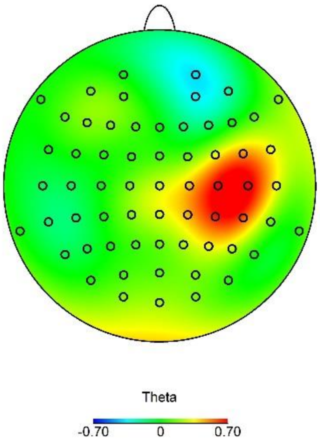
Theta participates in the coordination of disperse cortical areas to enable information exchange between them (Cavanagh et al., 2014; Klimesch et al., 2006). Given the correlation of central theta with alpha asymmetry (see Chapter III), it was proposed that theta reinforces the parietal asymmetry necessary for performing in Pong. Different individual theta distributions might reflect that an additional cortical area requires mediation with parietal cortex. For example, the left frontal theta enhancement in participants 6 and 23, overlapping with dorsolateral prefrontal cortex, could reflect the need to inhibit mirroring the ball’s movement with the paddles, so that theta modulates alternation between this area and right parietal association areas necessary for tracking the ball. Future research should address this issue by including a questionnaire at the end of the task, to evaluate the strategy of each participant.

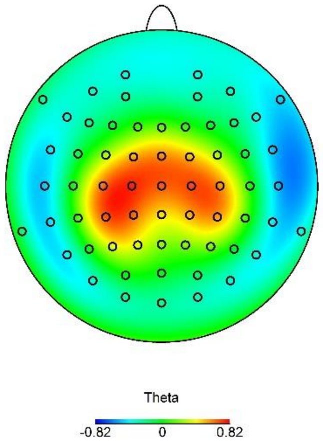
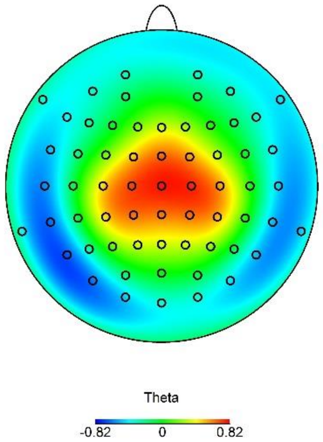
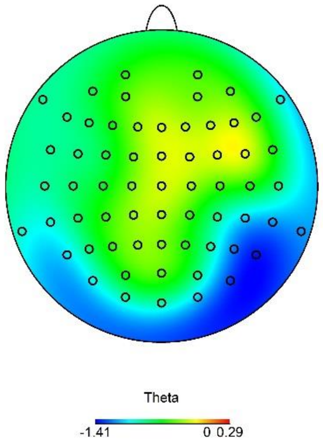
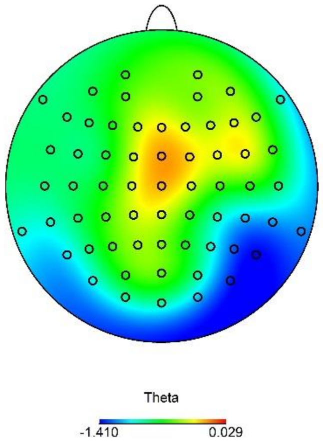
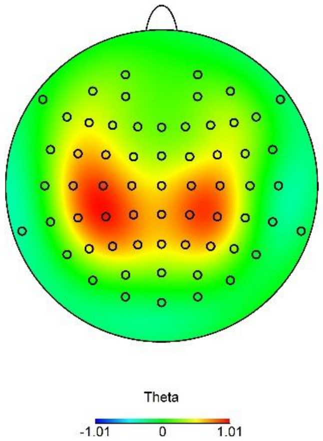
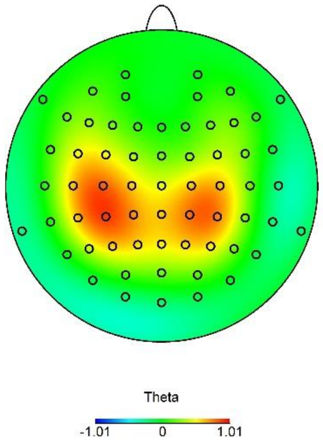
#	Stress-Free Block	Stress Induction Block
Av.	Mean Performance: **8180.37 ms**  	Mean Performance: **9752.67 ms** 

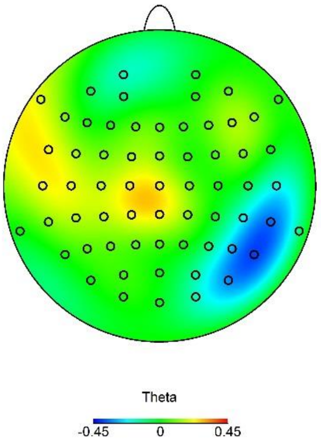
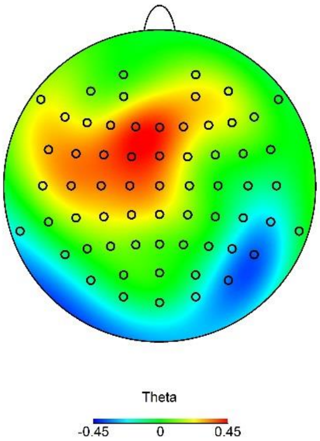
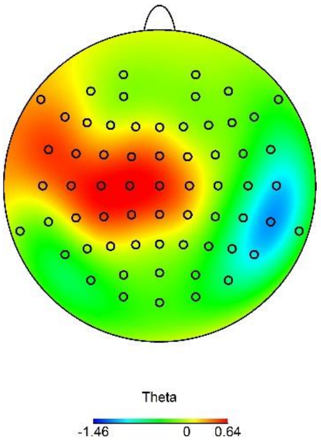
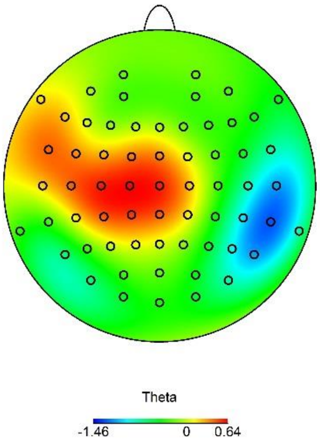
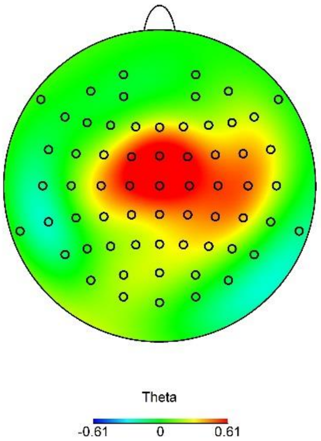
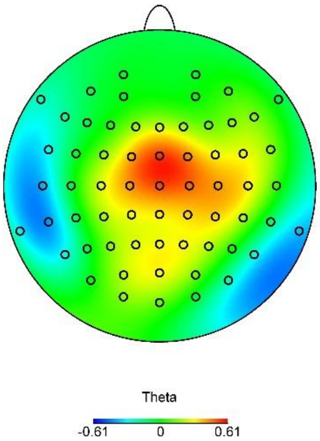
#	Stress-Free Block	Stress Induction Block
2	Mean performance: **8061.60 ms**  	Mean performance: **10978.60 ms** 
3	Mean performance: **4691.33 ms**  	Mean performance: **4183.60 ms** 
4	Mean performance: **3223.33 ms**  	Mean performance: **7439.80 ms** 

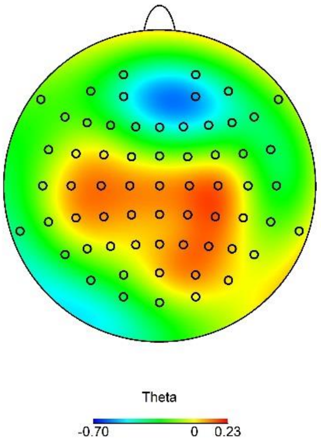
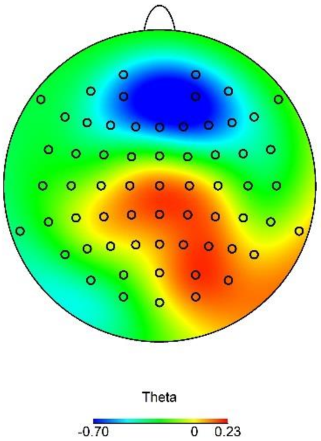
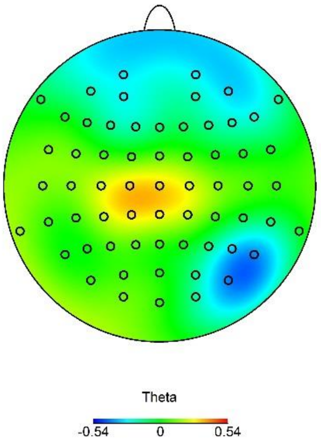
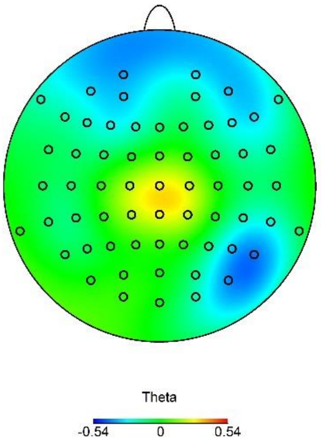
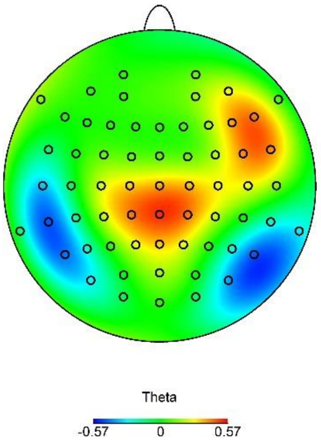
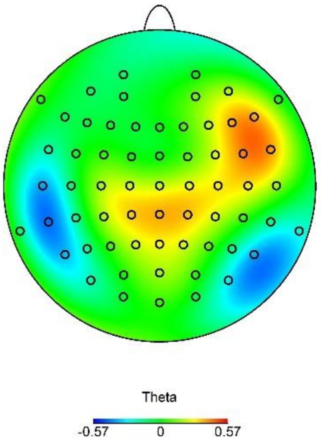
#	Stress-Free Block	Stress Induction Block
6	Mean performance: **6764.07 ms**  	Mean performance: **5189.53 ms** 
7	Mean performance: **5554.87 ms**  	Mean performance: **6059.27 ms** 
8	Mean performance: **5734.40 ms**  	Mean performance: **7092.40 ms** 

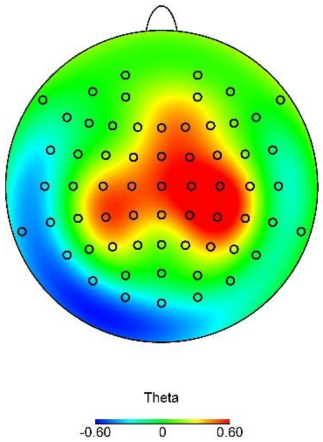
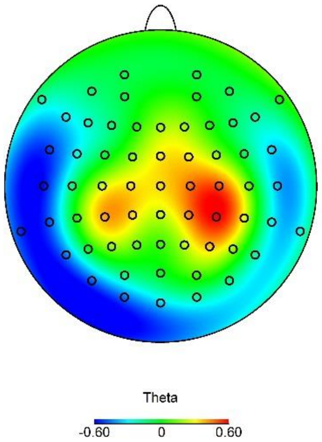
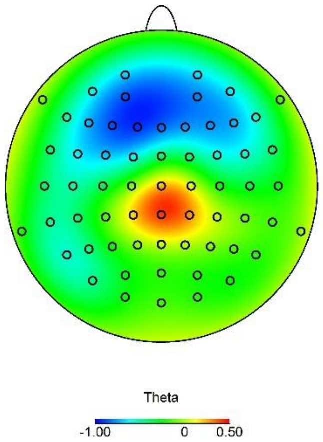
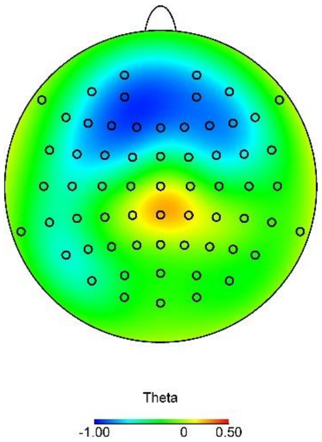
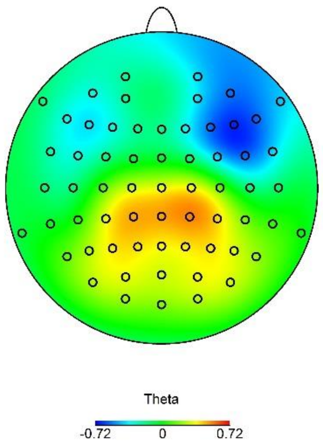
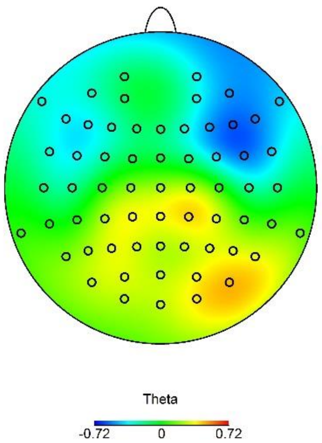
#	Stress-Free Block	Stress Induction Block
9	Mean performance: **3054.73 ms**  	Mean performance: **4331.53 ms** 
10	Mean performance: **10473.80 ms**  	Mean performance: **8908.60 ms** 
11	Mean performance: **22649.47 ms**  	Mean performance: **17196.47 ms** 

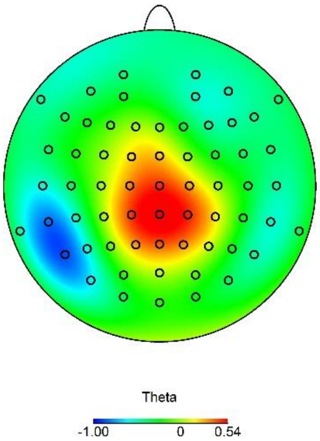
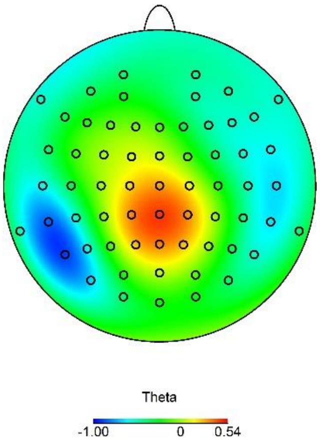
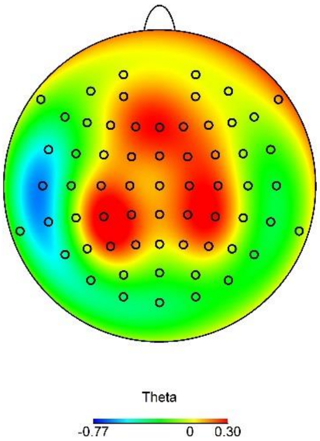
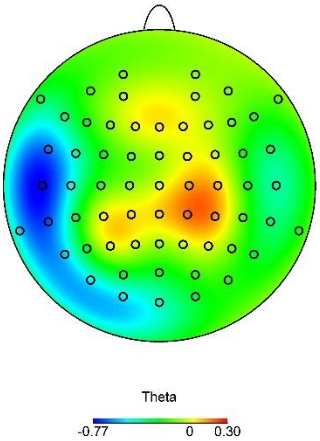
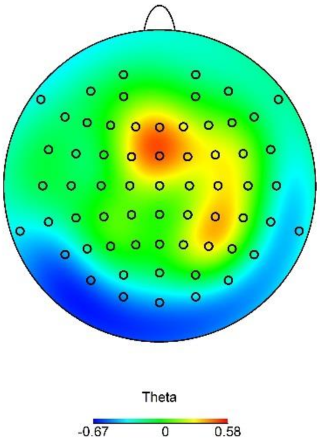
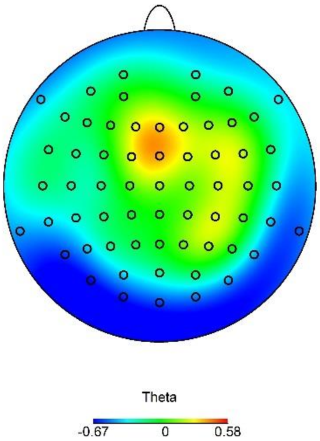
#	Stress-Free Block	Stress Induction Block
13	Mean performance: **3479.67 ms** 	Mean performance: **4242.73 ms** 
14	Mean performance: **10077.20 ms** 	Mean performance: **14344.93 ms** 
15	Mean performance: **3997.73 ms** 	Mean performance: **3119.80 ms** 

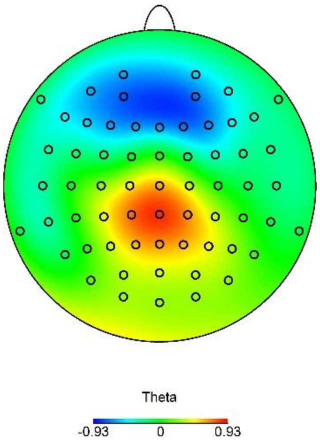
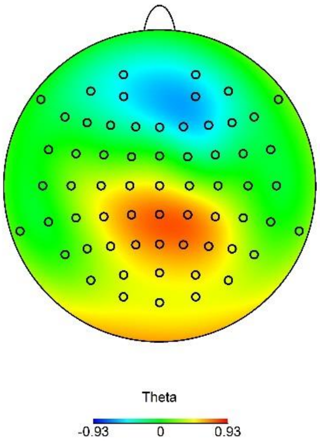
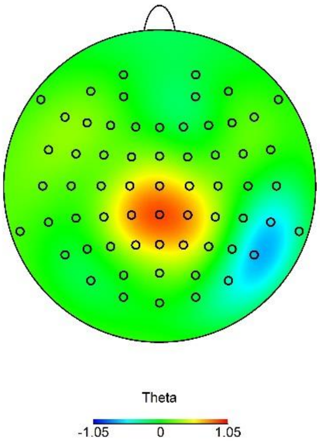
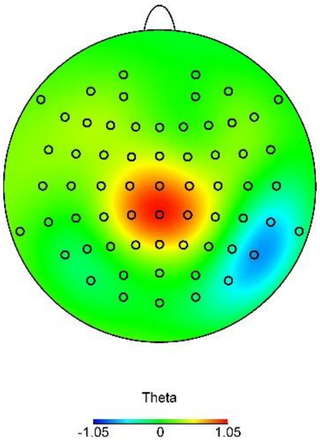
#	Stress-Free Block	Stress Induction Block
17	Mean performance: **4003.93 ms**  	Mean performance: **5191.07 ms** 
18	Mean performance: **8316.20 ms**  	Mean performance: **7437.33 ms** 
19	Mean performance: **7371.53 ms**  	Mean performance: **8045.07 ms** 

#	Stress-Free Block	Stress Induction Block
20	Mean performance: **16001.27 ms**  	Mean performance: **16686.20 ms** 
23	Mean performance: **6674.80 ms**  	Mean performance: **7179.07 ms** 
24	Mean performance: **4604.13 ms**  	Mean performance: **7696.73 ms** 

#	Stress-Free Block	Stress Induction Block
25	Mean performance: **11452.40 ms** 	Mean performance: **15727.20 ms** 
26	Mean performance: **18936.47 ms** 	Mean performance: **24673.07 ms** 
27	Mean performance: **16179.53 ms** 	Mean performance: **27466.40 ms** 

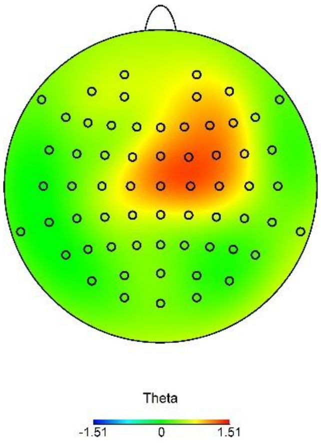
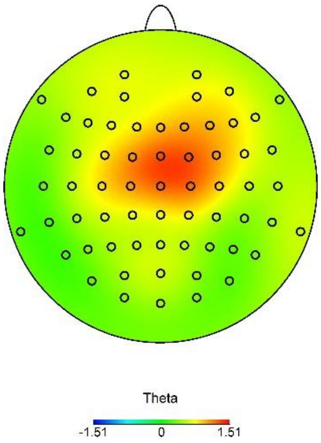
#	Stress-Free Block	Stress Induction Block
28	Mean performance: **7975.13 ms**  	Mean performance: **7526.93 ms** 
29	Mean performance: **14448.00 ms**  	Mean performance: **17024.93 ms** 
30	Mean performance: **5209.80 ms**  	Mean performance: **5798.20 ms** 

#	Stress-Free Block	Stress Induction Block
31	Mean performance: **10391.13 ms**  	Mean performance: **13053.07 ms** 
32	Mean performance: **2966.27 ms**  	Mean performance: **5801.13 ms** 
33	Mean performance: **7284.60 ms**  	Mean performance: **9167.80 ms** 

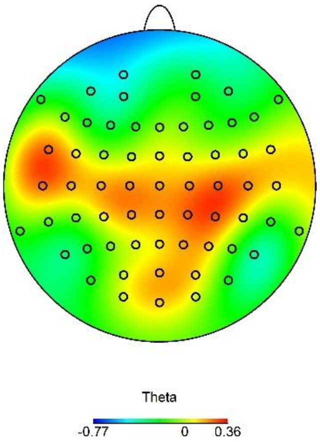
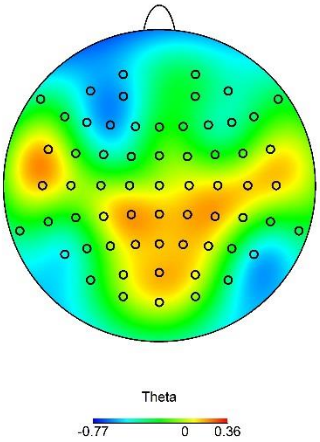
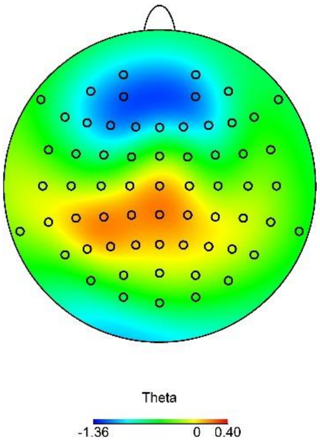
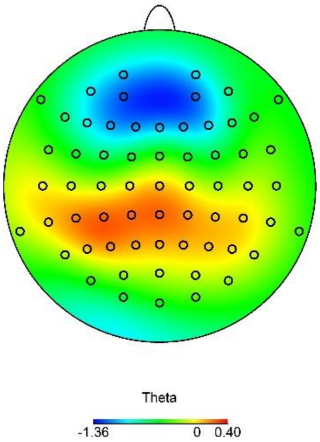
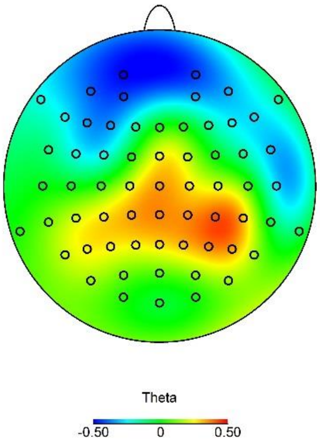
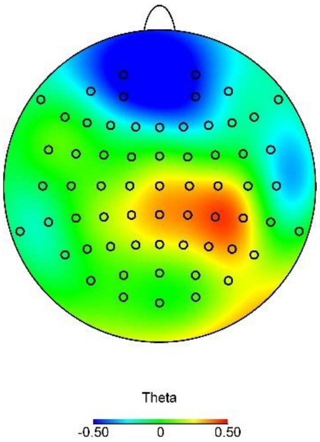
#	Stress-Free Block	Stress Induction Block
35	Mean performance: **3222.20 ms**  	Mean performance: **6928.00 ms** 
36	Mean performance: **4431.27 ms**  	Mean performance: **4338.00 ms** 

Excluded participants

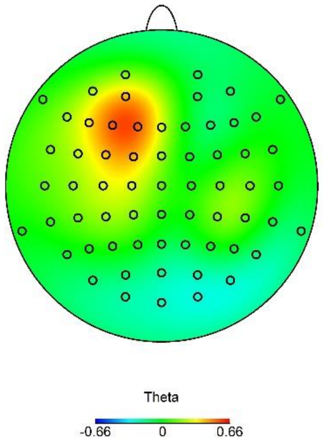
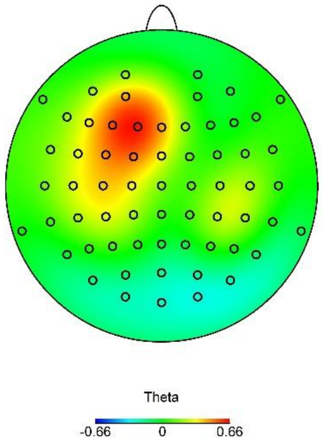
- Insufficient performance in training.

#	Stress-Free Block	Stress Induction Block
1	Mean performance: **2707.53 ms**  	Mean performance: **3987.40 ms** 

- Mild left-handedness

#	Stress-Free Block	Stress Induction Block
5	Mean performance: **3828.67 ms** 	Mean performance: **12340.60 ms** 
16	Mean performance: **9701.73 ms** 	Mean performance: **10203.40 ms** 
21	Mean performance: **6242.73 ms** 	Mean performance: **7524.40 ms** 

- Performance outlier

#	Stress-Free Block	Stress Induction Block
12	Mean performance: **33140.07 ms**  	Mean performance: **39531.27 ms** 

Chapter 5

General Discussion

The work presented in this dissertation concerned firstly with the electroencephalographic investigation of the cortical aftereffects of dynamic handgrip as a substrate of the multiple behavioral aftereffects reported in the literature after the handgrip exercises (Beckmann et al., 2013; Gable et al., 2013; Propper et al., 2013; Goldstein et al., 2010; Peterson et al., 2008; Harmon Jones, 2006; Schiff et al., 1998), especially regarding the prevention of skill-failure in sports performance under pressure reported by Beckmann et al., (2013). The subsequent aim was to test such preventive effects in a dynamic laboratory task analogous to the nature of most sports, the video game “Pong”, while assessing EEG. The main finding was a widespread reduction of resting cortical activity after dynamic handgrip with the left hand. It was proposed that this state would facilitate task-related activations once engaging in performance. In the next experiment, it was not possible to test the preventive effects of this induced state over performance under stress, because stress induction did not reduce performance in the control groups. However, it was noted that greater levels in the EEG theta band, an indicator of top-down cognitive control, were detrimental for performance in Pong. In this chapter, the results of these experiments are summarized and contextualized with each other, as well as in the larger frame of the literature. Future directions and practical effects are outlined.

5.1 Cortical activity during and after contractions and its implications

It was shown on Chapter 2 that after the execution of dynamic handgrip for 45 seconds with the left hand, an above baseline enhancement of resting alpha amplitudes (8-12 Hz) was produced, while the right hand produced a smaller, non-significant enhancement (Cross-Villasana et al., 2015). Alpha levels remained elevated for the whole two minute assessment period after handgrip, which reflect a long lasting reduction of cortical activity (Sauseng et al., 2009; Romei et al., 2008; Klimesch et al. 2006; Pineda, 2005). This is the first time that this aftereffect is measured with whole scalp EEG, similar observations had been made with TMS but were restricted to the motor cortex (Bäumer et al., 2002; Zanette et al., 1995; Bonato et al., 1996; Brasil-Neto et al., 1993). The current result has relevant psychophysiological implications.

In the psychological domain, the cortical aftereffects of dynamic and static handgrip had been previously inferred based on the behavioral outputs after contractions, and on results from event-related studies of single hand contractions, which differ from tonic and dynamic contractions (Liepert et al., 2001; Liu et al., 2003; Yang et al., 2011). In this way, it had been thought that handgrip exercises produced a biased activation asymmetry towards the contralateral hemisphere, which persisted after contractions ended (e.g. Beckmann et al., 2013; Propper et al., 2013; Schiff et al., 1998). In those psychological studies of handgrip where EEG was included (Gable et al., 2013; Peterson et al., 2008; Harmon-Jones, 2006) contralateral activation asymmetry during contractions was evidenced, but due to the interest in testing behavioral aftereffects, the period after contractions was not assessed, so that cortical aftereffects were still assumed from behavior. Currently, no significant modulations of asymmetry were observed at any phase (see next paragraph). Therefore, it is likely that behavioral aftereffects in other experiments could be explained in terms of an induced enhancement of alpha after the left hand contractions. For instance, the enhancement of memory retrieval after left contractions reported by Propper et al. (2013) could result from greater levels of alpha after contractions instead of the proposed right hemispheric dominance induction. Higher alpha levels before retrieval facilitate memory scanning due to less interference from irrelevant cortical activations (Klimesch et al., 2006). In the same way, the facilitation of sportive performance under stress after left handgrip in Beckmann et al. (2013) would result from enhanced alpha levels which reduce task-irrelevant activity produced by stress (Lee & Grafon, 2015; Linder et al., 1998), and facilitate task-related activations (Cheron, 2016; Hatfield et al., 2004; Haufler, 2000; Collins et al., 1990). It is generally supported that greater alpha amplitudes facilitate the brain's engagement in subsequent information processing (Doppelmayr et al., 1998; Jensen et al., 2010; Klimesch, 1999; Klimesch et al., 2006; Pineda et al., 2005).

It calls attention that in the current work, no contralateral activation asymmetry was observed during contractions, as in the three other EEG handgrip studies in the psychology domain (Gable et al., 2013; Peterson et al., 2008; Harmon-Jones, 2006). The latter studies placed the online EEG reference on the left mastoid, which enhances small differences between the two sides, even when further re-referenced to linked mastoids. This was in contrast to the current online reference over the midline. They further used a between-subjects design with large numbers of participants, in contrast to the current within-subjects design. It is possible that minor differences between the hemispheres are only detectable under such conditions. Still, in the study by Peterson et al. (2008) 12 out of 36 participants were removed for not showing the asymmetry effect. In the current work, not even a reference-free surface Laplacian showed asymmetry modulations (Chapter 2, Fig S4), giving strength to the result. Tonic or otherwise high-force contractions are known to produce bilateral activations (Wassermann et al., 1994; Liepert et al., 2001; Liu et al, 2003; Yang et al., 2011), and refined methods show that even during single hand contractions, ipsilateral inhibition is limited to a 100 ms window (Liepert et al., 2001) and is confined to the primary motor cortex (Nirkko et al., 2001). In that way, a blocked measurement of dynamic or static contractions shows a net bilateral excitation on the EEG (e.g. Deiber et al., 2001).

In the physiological domain, apart from the aforementioned long lasting cortical inhibition, two classical findings from event-related studies of single contractions were replicated (Fig 5.1). Firstly, during the contractions period with any hand, alpha modulations indicated an inhibition of the occipital region (increase of alpha amplitude) simultaneous to the bilateral motor activation (decrease of alpha amplitude). This observation is similar to that of Pfurtscheller and Lopes da Silva (1999), who also report simultaneous motor activation and occipital inhibition during single hand contractions (Fig 5.1-A). According to Pfurtscheller and Lopes da Silva this simultaneous excitation and inhibition result from the interplay of excitatory thalamic relay cells and the inhibitory neurons of the reticular nucleus, which respectively excite the cortical neurons involved in the movement, and inhibit cortical areas not relevant for it. The currently observed inhibition (Fig 5.1-B) indicates that this effect is consistent with both hands, and persists during repetitive hand contractions, so that no adaptation process occurs. If this inhibition happens around each contraction of dynamic handgrip a net occipital alpha enhancement is observed. An occipital inhibition is also observable in Deiber et al. (2001), during finger movement sequences (Chapter 1, Figs 1.4 and 1.5), although it was not analyzed by these authors. Together, all these observations with different kinds of movements support the transient inhibition of the visual cortex during motor execution.

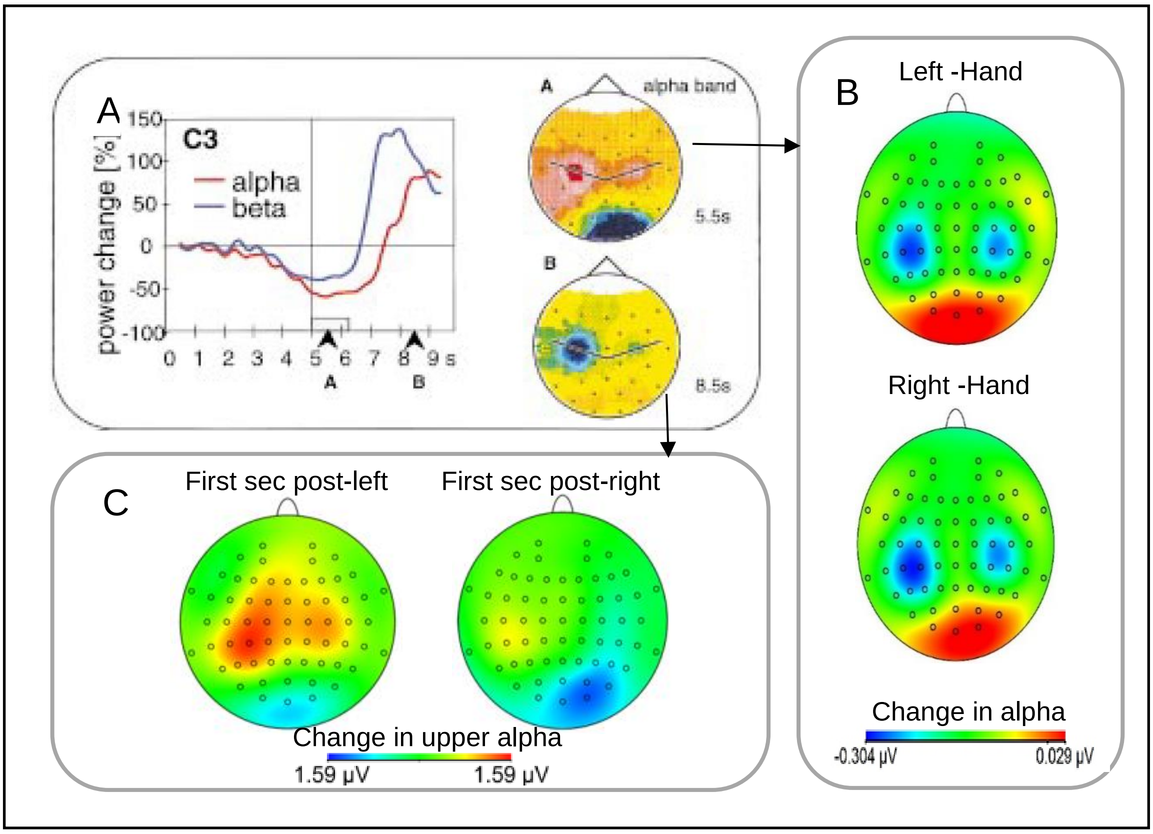


Fig 5.1. Comparison of scalp alpha band patterns during and immediately after single hand contractions (Pfurtscheller and Lopes da Silva, 1999), and dynamic handgrip (Cross-Villasana et al., 2015). Relevant comparisons are indicated with arrows. A) Grand average event-related-desynchronization (ERD) curves calculated in the alpha and beta bands in a right hand movement task (left side). Grand average maps calculated for a 125 ms interval during movement (A) and after movement (B) (right side). Red color indicates greater ERD (alpha suppression), and blue color indicates negative ERD (alpha enhancement). Adapted from Pfurtscheller and Lopes da Silva (1999) with permission. B) Grand average maps of alpha (8 – 12 Hz) amplitude during dynamic handgrip of the left and right hand, obtained through subtraction of baseline from contractions. Blue color indicates alpha suppression, and red color indicates alpha enhancement. Adapted from Cross-Villasana et al (2015) with permission. C) Grand average maps of upper alpha (10 – 12 Hz) in the first second after contractions, obtained through subtraction of the last second of contractions from the first second after contractions. Adapted from Cross-Villasana et al (2015) with permission.

The second replicated effect concerns the cortical reaction immediately following movement termination. In the first second after contractions, a rebound of the upper alpha band (10-12 Hz; also known as “Mu Rhythm”) was observed, in accordance with Pfurtscheller and Lopes da Silva (1999) (Fig 5.1-C), reflecting the onset of inhibitory mechanisms on the sensorimotor cortex after movement termination. As can be observed in (Fig 5.1-C) the rebound was greater after left hand contractions, parallel to what was observed for the whole two minute post-contraction period. Indeed, as noted in Chapter 2, this initial upper alpha enhancement extended to the whole alpha band and towards the rest of the scalp afterwards, constituting the reported long lasting inhibition (Cross-Villasana et al., 2015). Interestingly, occipital regions showed alpha suppression immediately after contractions (Fig 5.1-C), indicating an end to the active inhibition they showed during contractions, but their alpha levels were still above baseline and continued to increase along the two minute post-contraction period (Chapter 2, Table 3), contributing to the whole-scalp post-contraction inhibition.

It was argued on Chapter 2 that the long lasting inhibition results from the action of cortical inhibitory interneurons which first activated during contractions in order to control cortical excitability (Nunez et al., 2014; Pfurtscheller & Lopes da Silva, 1999; Salenius et al., 1997; Salmelin et al., 1994), prevent the spread of activity (Schevon et al., 2012; Bloom et al., 2005; Alarcón et al., 1994) and provide movement specificity (Sohn et al., 2004; Pfurtscheller & Lopes da Silva, 1999). And that these mechanisms continued to be active once movement was terminated, producing a generalized reduction of activity (Bonato et al., 1996; Zanette et al., 1995). These mechanisms are mostly evidenced by clinical conditions where their action is deficient, mainly in epilepsy. In epileptic patients continuous movements like coloring, brushing teeth, or clenching a fist can produce inter-ictal epileptiform activity or even trigger an ictal episode (Takahashi et al., 1993). After single hand movements, epileptic patients also take considerably longer to normalize cortical activity on frontal and motor regions compared to healthy participants (Derambure et al., 1997). In-vitro studies have shown that when seizures fail to spread, the ictal focus still affects surrounding regions before they normalize through local inhibitory mechanisms. Such mechanisms are the same present in healthy population, such as in Chapter 2, and also restrict less intense forms of activity (Trevelyan et al., 2006).

The continued inhibitory effect post-contractions has been previously observed in TMS studies with other repetitive hand movements, where cortical excitability was reduced with times spans up to 30 minutes after movement (Bäumer et al., 2002; Bonato et al., 1996; Zanette et al., 1995; Brasil-Neto et al., 1993). The EEG alpha band is an analogous indicator of cortical activity to TMS excitability (Sauseng et al., 2009; Romei et al., 2008; Klimesch et al. 2006). The use of EEG however, overcomes the limitation of TMS to the motor cortex, and the whole scalp can be monitored simultaneously. In this way it was shown for the first time that the aftereffects previously observed in TMS experiments concern larger areas of the cortex, and are generally larger after left hand contractions. In the current work it is proposed that a larger inhibitory effect after left hand contractions is due to the right hemisphere, which mostly drives the left hand, having a broader range of connections within itself, and with the left hemisphere (Iturria-Medina et al., 2011; Allen et al., 2003; Tucker et al. 1986; Scheibel et al., 1985; Seldon, 1982; Gur et al., 1980), so that inhibitory mechanisms are triggered to a greater extent.

Finally the elevated alpha levels induced through dynamic handgrip were similar in magnitude to those induced through brain modulation techniques such as repetitive TMS (rTMS; Klimesch et al.,

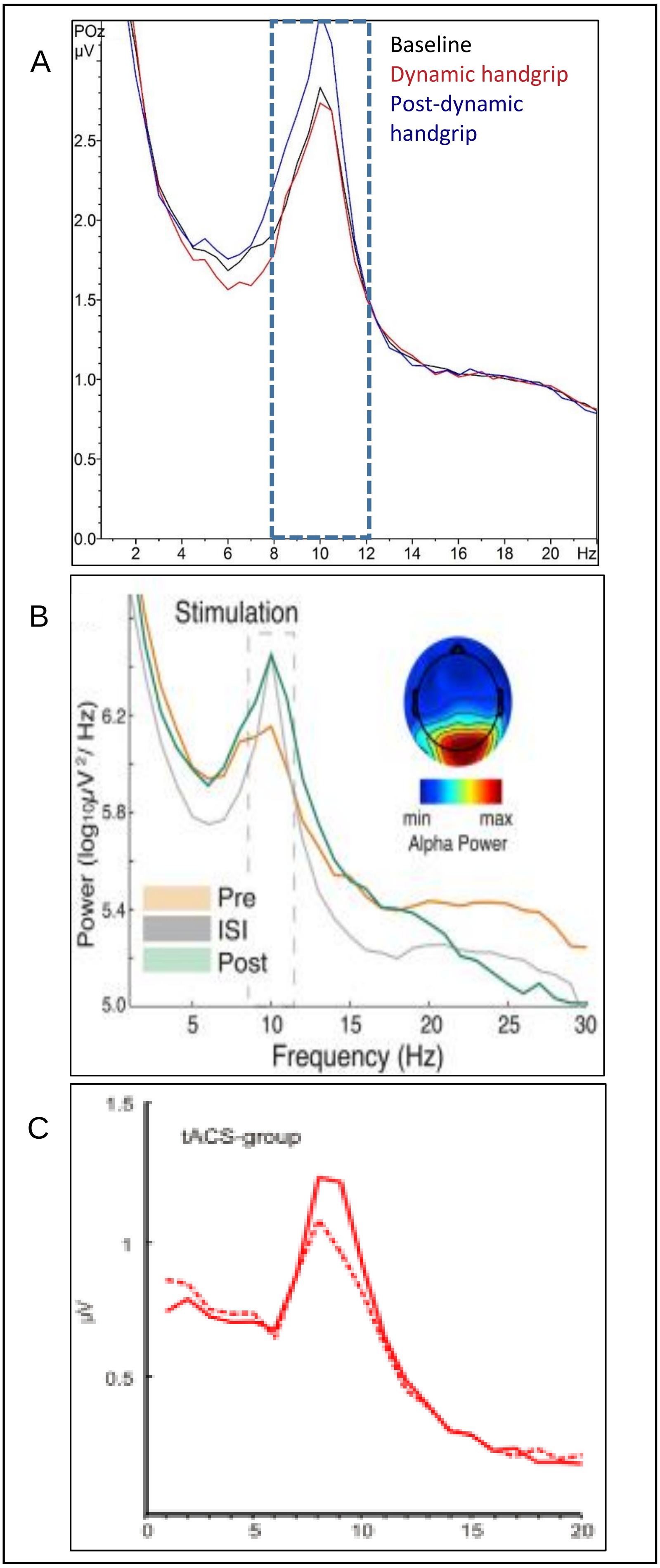


Fig 5.2. Spectral plots comparing the enhancement of alpha amplitudes induced through left-dynamic-handgrip and through tACS as seen in their respective group averages.

A) Group averaged amplitude levels at electrode POz from the experiment in Chapter II; during a 2 min baseline, through 45 sec of left-dynamic-handgrip, and during a 2 min post-handgrip measurement. The alpha band (8-12 Hz) is enclosed in the rectangle.

B) Grand average of power spectra during 20 min of 10 Hz tACS (ISI) along with 1 min pre and post stimulation measurements at electrode POz. Adapted from Helfrich et al. (2014) with permission.

C) Group averaged EEG amplitude on a 3 min baseline measurement (dashed line) and a 3 min measurement after 10 minutes of tACS (solid line). Adapted from Zaehle et al. (2010) with permission.

2003) or transcranial alternating current stimulation (tACS; Zaehle et al., 2010; Helfrich et al., 2014). Fig 5.2 displays spectral plots at electrode Pz showing the increase in alpha amplitudes obtained after left hand contractions, compared to that obtained through tACS in other studies (Zaehle et al., 2010; Helfrich et al., 2014). In all cases, the specificity of aftereffects to the alpha band is evident. Given this similarity, it is worth pondering potential clinical uses of dynamic handgrip like those proposed for tACS and rTMS, especially regarding disorders associated with abnormalities of cortical oscillations such as Parkinson's disease or neuropsychiatric disorders like attention-deficit/hyperactivity disorder (Helfrich et al., 2014; Woltering et al., 2012; Zaehle et al., 2010; Klimesch et al., 2003).

5.2 Future directions of dynamic handgrip

When considering potential clinical uses of dynamic handgrip it is necessary to explore long term effects over cortical activity, in the order of days or weeks, which continued practice of the exercise could produce (e.g. a permanent increase of resting alpha amplitude). As mentioned in Chapter 1, such kind of long term effects through handgrip routines have been reported for the cardiovascular system. When regularly executing handgrip exercises, moderate but consistent reductions in resting systolic blood pressure have been observed in in hypertensive patients (Brook et al., 2013; Millar et al., 2009) as well as in healthy population (Ray & Carrasco, 2000; Millar et al., 2009-2). These cardiovascular modulations have been presumed of neural origin (Millar et al., 2009-2; Sinoway et al., 1996). In that sense, the routines used in cardiology studies could be adopted to explore their effects over the cortex, for example: 4 repeated 2-minute-long bouts performed 3 times per week (Brook et al., 2013).

In the case of the cortex, so far it appears that the aftereffects are differential with each hand. As seen on Chapter 2, in average alpha enhancements were greater after left hand contractions in right handers, but a few participants showed the opposite pattern, which is not noticeable in the group average. This is an important consideration for any clinical or sportive application. In those cases, an alternating or bilateral contraction scheme could be useful. In Chapter 2, the aftereffect of left contractions was not cancelled out in the sub-group where right contractions followed, as seen in Fig S1 in Chapter 2 (Cross-Villasana et al., 2015). Deiber et al. (2001) report higher activation profiles for left and bilateral finger sequences than for right sequences, it is then expectable that post-movement inhibition of bilateral movements could be similar to the one currently observed after left contractions. Finally, since dynamic and static handgrip show similar activation profiles during their execution (Liu et al., 2003), it appears safe to assume that the currently observed aftereffects of dynamic handgrip extend to static handgrip.

In the psychological domain, it is still necessary to clarify the behavioral aftereffects of dynamic handgrip. With knowledge of the post-handgrip alpha enhancement, a logical following step in this direction would be to test the same tasks used in studies with other alpha induction techniques, such as mental rotation after rTMS (Klimesch et al., 2003), or oddball after tACS (Helfrich et al., 2014;

Doppelmayr, 1998). These tasks have the advantage of being standards in neurocognitive research, and can be further linked to modulations in event-related potentials/synchronization/desynchronization.

The immediate aftereffects of dynamic handgrip appear promissory to be incorporated in the pre-performance routines of athletes, but as mentioned above, the form of the handgrip, time span of effects, and behavioral effects need to be precisely determined. The Pong game as a dynamic task analogous to sports is closer to the application of dynamic handgrip in the field. Currently stress-induction was not effective in affecting task performance, but other modifications can be done to the Pong task to test the effects of dynamic handgrip, this is discussed following section.

5.3 The Pong game and the theta band as research tools for performance in complex tasks

The Pong game was chosen as a laboratory task given its requirements similar to most sports, such as the need to continuously monitor a broad space and making adjustments to changing circumstances. Rightwards alpha asymmetry (Rebert & Low, 1978) and central theta enhancements (Rebert et al., 1984) had also been identified related to the task, which are respectively in accordance with research in visuospatial tasks (Janelle & Hatfield, 2008; Kerick, 2007; Kramer et al., 2007; Del Percio et al., 2009; Hatfield et al., 2004) and in complex tasks such as driving (Borghini et al., 2014; Borghini et al., 2012; Touryan et al., 2016). These characteristics put Pong in advantage over standard neurocognitive paradigms in order to test the effects of stress on performance with greater ecological validity. Unfortunately, the stress induction did not affect performance and all groups improved during the stress block, so that the preventive effects of left dynamic handgrip could not be tested. Nonetheless, when analyzing all participants as one group, the EEG markers of the task were replicated and further analysis allowed to put them in context with task performance.

On chapters 3 and 4, task-related enhancements in central theta power were generally related to poorer performance. In the first, stress-free block, theta enhancements showed a moderate negative correlation with Pong trial duration. In the second block with stress induction, performance improved and theta amplitudes decreased in relation to the first block. Together, these observations support that greater theta enhancements are detrimental for performance in this task. Theta and performance did not reach significant correlations in the second block, but this owes to less variability in the data due to experimental manipulation. As mentioned in Chapter 4, using the participant's own stress-free average as a performance criterion in the second block may have unintendedly served as goal setting (Locke & Latham; 2002) which improved performance and reduced theta levels. This improvement likely owes to enhanced alertness levels, reflected by the unpredicted reduction of posterior theta (Beatty et al., 1974; Lin et al., 2010), greater during the stress block (Chapter 4, Fig 4.2).

Central theta is supported to be a marker of top-down control exertion (Cavanagh & Frank, 2014; Anguera et al., 2013; Sauseng et al., 2007; Inanaga, 1998). Under such premise, it is currently proposed that performance in dynamic tasks such as Pong is more proficient under a bottom-up guidance of attention, with the least top-down control possible. In a psychological sense, this observation befits the model of motor-skilled acquisition by Fitts and Posner (1967) in which at first, the performer at exerts great cognitive effort to control execution, but as more experience is gained, control is relegated to passive mechanisms, allowing for automatization of the task (Hatfield et al., 2004; Milton et al., 2004; Haufler, 2000). On Chapter 3, more skilled participants showed lesser increments in theta, it was argued that they might have achieved greater automaticity of performance. Beckmann et al. (2013) propose that when skills of experienced performers break down under pressure, they regress from the automatic to the cognitive phase. In this way, enhancements in theta levels can be used as markers of such regression.

The proposal of Beckmann et al. (2013) is supported mostly on studies of event-related alpha band modulations during self-paced tasks such as marks shooting and golf-putting. These studies show that better performance is related to greater right parietal activation related to visual processing, and lesser left frontal and temporal activation related to conscious control and language (Janelle & Hatfield, 2008; Del Percio et al., 2009; Hatfield et al., 2004; Deeny et al., 2003; Haufler, et al. 2000; Salazar, 1990). In the current non-self-paced task, right parietal activation was observed but it was not sufficiently sensitive to performance levels. To achieve this sensibility during a dynamic task, more refined methods would be required to capture the fast-paced nature of alpha modulations while performing. For instance, event markers could be added at each paddle hit to analyze alpha modulations around it, or band-filtered data could be tracked at each sample point. For the current purpose however, theta was a robust marker of performance, as it reflects a single process at a constant location, that is, cognitive control observable over the midline.

According to Cavanagh et al. (2014), the mechanism of cognitive control reflected by theta, consists on the coordination of disparate cortical regions through the mid-cingulate cortex after the need for control is first triggered by the mid-prefrontal cortex. In Pong, a minimal degree of theta enhancement as noted by Rebert et al. (1984) would be expectable to coordinate between visual and motor areas for tracking the ball and adjusting the paddles respectively. Any additional cortical processes would require greater coordination between them and further increase theta amplitudes. For example, if a non-proficient performer consistently used verbal cues to guide performance, additional coordination of the visual and motor regions would be necessary with language areas of the left temporal cortex, increasing theta amplitude further. The same could be expected if the proficient performer regressed from the automatic to the cognitive phase of performance of the model of Fits and Posner (1967) due to the effects of pressure to perform (Beckmann et al., 2013). The theta modulations reflecting this process average into the midline and produce a consistent signal in the group’s mean. If the individual scalp maps are explored, diverse deviations from the midline are revealed, which were consistent along the two blocks (Chapter 4 Annex). Most likely these patterns reflect the different kinds of strategies or difficulties in each participant during the task (e.g., self-talk, impulse inhibition, self-monitoring). But most importantly, they all have a common midline component which gives strength to the theta signal, and allows it to differentiate performance levels, unlike the more variable alpha modulations.

5.4 Use of theta in future handgrip experiments

It has been mentioned that theta indicates control processes to coordinate different cortical regions, and that either unexperienced performers or skilled performers under pressure involve more cognitive processes than are essential while performing, requiring then greater coordination among more cortical regions. In skilled performers, if dynamic handgrip before performance enhances alpha levels, hence ameliorating these additional processes (e.g. self-talk), lesser theta levels and better performance would be expected in the subsequent task. In event-related studies, factors like self-talk are suggested based on asymmetric alpha activations, but in dynamic tasks such as Pong, these asymmetries were not consistent enough to correlate with performance. Hence, the use of theta is recommended as an EEG marker of performance to evaluate the effects of stress and learning in complex tasks.

Importantly, the stress induction method needs to be improved to generate sufficient stress levels that produce skill failure in the task. Alternatively, factors within the task could be modified to make it more stressful. For example, a gradual increase of speed of the ball as the trial gets longer. It is not recommended to use the participant’s own stress-free performance as a criterion under the stress block, since it appears to be a facilitator of performance through goal setting. Alternative criteria could be a general criterion presented to all participants that is too demanding or almost impossible, or the participant’s performance augmented by a factor of three for example.

5.5 A final note: the alpha arrest reaction

Alpha suppression when opening the eyes, otherwise known as “arrest reaction” (Cheron et al., 2016), was moderately predictive of subsequent performance in Pong, with a smaller arrest reaction correlating with longer trial duration. Higher resting alpha levels allow for greater task-related suppression (Doppelmayr et al., 1998; Jensen et al., 2010; Klimesch, 1999; Klimesch et al., 2006; Pineda et al., 2005). Therefore, if alpha levels remain elevated after eye opening, more space is available for further task-related suppression (Cheron et al., 2016). During the stress block, alpha suppression was greater, and the correlation coefficients with the arrest reaction were higher (Chapter 4, Table 4.2), supporting the impact of resting alpha on performance. These observations further support the rationale behind dynamic handgrip: increasing alpha levels before performance.

By themselves, open-eyes resting alpha levels had no predictive power on performance. This is due to factors other than brain activity affecting scalp EEG measurements, such as skull thickness or orientation of the dendrites which generate the signal. It was only through the contrast with the eyes closed state that correlation was achievable, since the perturbation produced by opening the eyes is purely due to brain activity. Correlation levels were medium most likely due to the complexity of the Pong game, in which participants had different skill levels despite training. If the task was trained to high proficiency in all participants, the correlation with the arrest reaction would likely be higher. Altogether, the current correlations support the proposal of Cheron et al. (2016) where the arrest reaction can provide an index about the global resting state activity of the athlete’s brain.

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RESEARCH INTERESTS

EEG, clinical electrophysiology, transcranial magnetic stimulation, rehabilitation

EDUCATION

Doctoral Candidate of Neuroscience
Graduate School of Systemic Neuroscience, Munich
October 2011 – Present
Disertation: Unimanual dynamic handgrip and its effect on the EEG alpha rhythm
Supervisor: (Prof. Jürgen Beckmann)

Master of Science in Neurocognitive Psychology
Ludwig Maximilians Universität, Munich
October 2009 – September 2011
Thesis: Electrophysiological Correlates of ADHD Compound Search Performance
Supervisor: (PD DR. Kathrin Finke, Dr. Thomas Töllner)

Licenciate (Diploma) in Psychology
Universidad Iberoamericana, Mexico City
August 2002 – December 2006
Thesis: Relationship between criminal behavior and Cattel's 16 personality factors
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PUBLICATIONS

Cross-Villasana F, Finke K, Hennig-Fast K, Kilian B, Wiegand I, Müller HJ, Möller HJ, and Töllner T. (2015): **The Speed of Visual Attention and Motor-Response Decisions in Adult Attention Deficit/Hyperactivity Disorder.** *Biol Psychiatry*

Cross-Villasana F, Gröpel P, Beckmann, J, (2015): **Unilateral Left-Hand Contractions Produce Widespread Depression of Cortical Activity after their Execution.** *PLOS One*

WORK EXPERIENCE

(Oct 2011 – Present) **Lehrstuhl für Sportpsychologie**, Fakultät für Sport und Gesundheitswissenschaft, Technische Universität München
Position: Scientific Co-Worker

- Doctoral Research Project "Unimanual dynamic handgrip and its effect on the EEG alpha rhythm", teaching, laboratory administrator.
- Investigated electrophysiological substrates of a psychological effect reported in the literature. Assembled the EEG laboratory; standardized the recording settings, procedure, and proposed a standard data pre-processing scheme.

(Feb 2010 – Aug 2011) **EEG & Behavior Lab**, Ludwig Maximilians Universität München, (Dr. Agnieszka Wykowska)
Position: Laboratory Assistant (HIWI)
• Recruiting of research participants and running experiments; organization of a team of student assistants, laboratory maintenance.
•Administrated the HIWI's schedules to increase efficiency.

(Oct 2006 – Sep 2009) **Centro Psicopedagógico Psicointegra**, private clinic, Mexico
Position: Psychological Evaluator
• Psychological assessment using psychometric tests, surveys and interview. Training for children with learning disabilities based on the psychological assessment. Planning and teaching of seminars about psychology and education for parents and teachers.
• Developed an Excel-based grading protocol for the psychometric tests.

ADDITIONAL TRAINING

Transcranial Magnetic Stimulation. (March 2014). Klinik für Klinische Neurophysiologie, Universitätsmedizin Göttingen. TMS of the motor cortex, TMS of the visual cortex, diagnosis with paired pulses.

Brain Vision Analizer, intermediate certificate. (Oct. 2013). Brain Products, Berlin. ERP, LORETA, ICA, wavelets.

Effective Grant Writing for Scientists. (March 2013). ProSciencia, Munich. Basics of grant applications, strategies for writing a successful grant.

Presenting Professionally. (May 2012). Graduate School of Life Science Munich. Soft skills in academic presentation.

Diagnostic Procedures in Neurology. (March 2012). Graduate School of Systemic Neuroscience, Munich. Primer on neurological diagnosis for: epilepsy, gait disorders, traumatic brain injury, hemi-spatial neglect, Parkinson's disease.

INTERNSHIPS AND VOLUNTARY SERVICES

- (Oct 2008 – Sep 2009) **Casa Hogar Alegría,** orphanage (Zinacantepec, Mex).

• Institutional psychological intervention (sponsored by Psicointegra clinic). Coordinated the diagnostic assessment, psychometric evaluation of 21 girls, brief counseling of 8 girls, interviews with the personnel.

- (Jun 2005 – Dec 2005) **Pro-Mazahua Patronage,** NGO (Atlacomulco, Mex). Helps the development of the Mazahua ethnic group.

• Carried field research about the effectiveness of a new educational program in local kindergartens. Carried a survey of the coverage of governmental programs.

LANGUAGES

Spanish (mother tongue); **English** (Advanced); **German** (Intermediate)

LIST OF PUBLICATIONS

Cross-Villasana F, Finke K, Hennig-Fast K, Killian B, Wiegand I, Müller HJ et al. (2015): The speed of visual attention and motor-response decisions in adult attention-deficit/hyperactivity disorder. *Biol Psychiatry* 78: 107 – 115.

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AFFIDATIV

Eidesstattliche Versicherung/Affidavit Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation „The cortical aftereffects of dynamic handgrip and the role of the electroencephalographic alpha and theta bands before and during visuomotor performance“ selbstständig angefertigt habe, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

München, den 01 Juli, 2016

I hereby confirm that the dissertation “The cortical aftereffects of dynamic handgrip and the role of the electroencephalographic alpha and theta bands before and during visuomotor performance” is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

Munich, 1st of July, 2016

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Unterschrift/Signature: **Fernando Cross Villasana**

AUTHOR CONTRIBUTIONS

Chapter 1 “Introduction: State of the art and preliminary work” was written by Fernando Cross-Villasana.

Chapter 2 “Unilateral left-hand contractions produce widespread depression of cortical activity after their execution” was published on the journal *PLoS One*. From the authors, Fernando Cross-Villasana designed the experiment with input from Jürgen Beckmann, Peter Gröpel and Michael Doppelmayr. The experiment was conducted by Fernando Cross-Villasana. Data was analyzed by Fernando Cross-Villasana under supervision from Jürgen Beckmann and Michael Doppelmayr. The article was written by Fernando Cross-Villasana and Peter Gröpel, and was revised and commented by Jürgen Beckmann and Michael Doppelmayr.

For Chapter 3, the Pong game was customized for its use in this experiment by Frank Häusler. Beta-testing, user experience inquiry, and standardization of the game were conducted by Fernando Cross-Villasana.

Pilot studies of the stress-induction method were designed and conducted by Fernando Cross-Villasana with input from Jürgen Beckmann and Peter Gröpel.

Chapter 3 “Theta amplitude as an indicator of performance proficiency in a dynamic visuospatial task” is a manuscript intended for the journal *Biological Psychology*. The experiment was designed by Fernando Cross-Villasana with input from Jürgen Beckmann and Peter Gröpel, based on the procedure used by the latter authors in field studies. The study was conducted by Fernando Cross-Villasana and Martina Siegert. The manuscript was written by Fernando Cross-Villasana and Peter Gröpel.

Chapter 4 “Stress induction improved performance and reduced theta amplitude” is based on the same data from Chapter 3, and was written by Fernando Cross-Villasana.

Chapter 5 “General Discussion” was written by Fernando Cross-Villasana.

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