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Final paper

Stimulating representations: Exploring the neural basis of Representational Momentum through transcranial Alternating Current Stimulation (tACS) in the Beta and Theta bands

Rappresentazioni stimolanti: Esplorazione delle basi neurali del Representational Momentum attraverso l'utilizzo di Stimolazione Transcranica a Corrente Alternata (tACS) nelle bande Beta e Theta

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Chapter 0 – Abstract

How does the brain predict the motion of a moving object? If a stimulus suddenly disappears in its smooth trajectory, the perceived vanishing point is displaced forward in the direction of motion. Such displacement has been referred to as Representational Momentum (RM) because it is thought that such displacement reflects the intrinsic momentum of the representations of real-world objects (Freyd and Finke, 1984; Hubbard, 2005, 2014). There are many variables related to this phenomenon, many types of RM, many paradigms to study this effect, various brain areas related to RM and motion perception and different theoretical approaches; all of this will be reviewed in the present work. In a recent study, Di Dona et al. (*in preparation*) found a correlation between beta-band activity (BBA) and the forward tilt of a rotating bar in a RM task. In this study, we used the same paradigm and stimuli as Di Dona et al., and we attempted to find a causal link between beta oscillations and RM with the use of transcranial alternating current stimulation (tACS). It has been found that tACS can entrain cortical neurons (Helfrich et al., 2014), that is it can align neuronal activity to an external frequency. We administered three different types of stimulation (beta-tACS, theta-tACS and sham) while participants performed an RM task. Contrary to expectation, the results showed no effect of stimulation on the RM effect and that beta-tACS lowered task accuracy. This can still demonstrate a functional specificity of BBA for motion perception. Future studies should try to use different motion perception tasks in order to understand the relationship between BBA and motion perception more deeply.

Chapter 1 – Theoretical introduction

1.1 The visual system

Seeing is one of the most complex tasks the brain performs constantly. In order to be able to see, several mechanisms need to take place in many different brain areas, both cortical and sub-cortical. Such mechanisms include motor processes that allow eye movements (i.e. saccades and smooth pursuit), sensory ones that allow visual information processing and attentional ones that filter the information. But before visual information reaches the brain, it has to pass through the eye.

1.1.1 From the retina to the primary visual cortex

Any object or set of stimuli in the visual world is first sensed by the eye. Everything that we see must have the property of reflecting light. Such reflected light has to pass first through the cornea to be refracted, then through the lens, which allows the eye to adjust the focus (i.e. accommodate) to different distances and to converge the rays precisely into the fovea, the location where the retina is thinnest. The fovea is the centre of the retina and is the place where most photoreceptors called "cones" lie. Photoreceptors are the only light-sensitive cells in the retina – and nearly in the whole nervous system. Light has to pass through the transparent layers of ganglion and bipolar cells before reaching photoreceptors. It is then absorbed by the

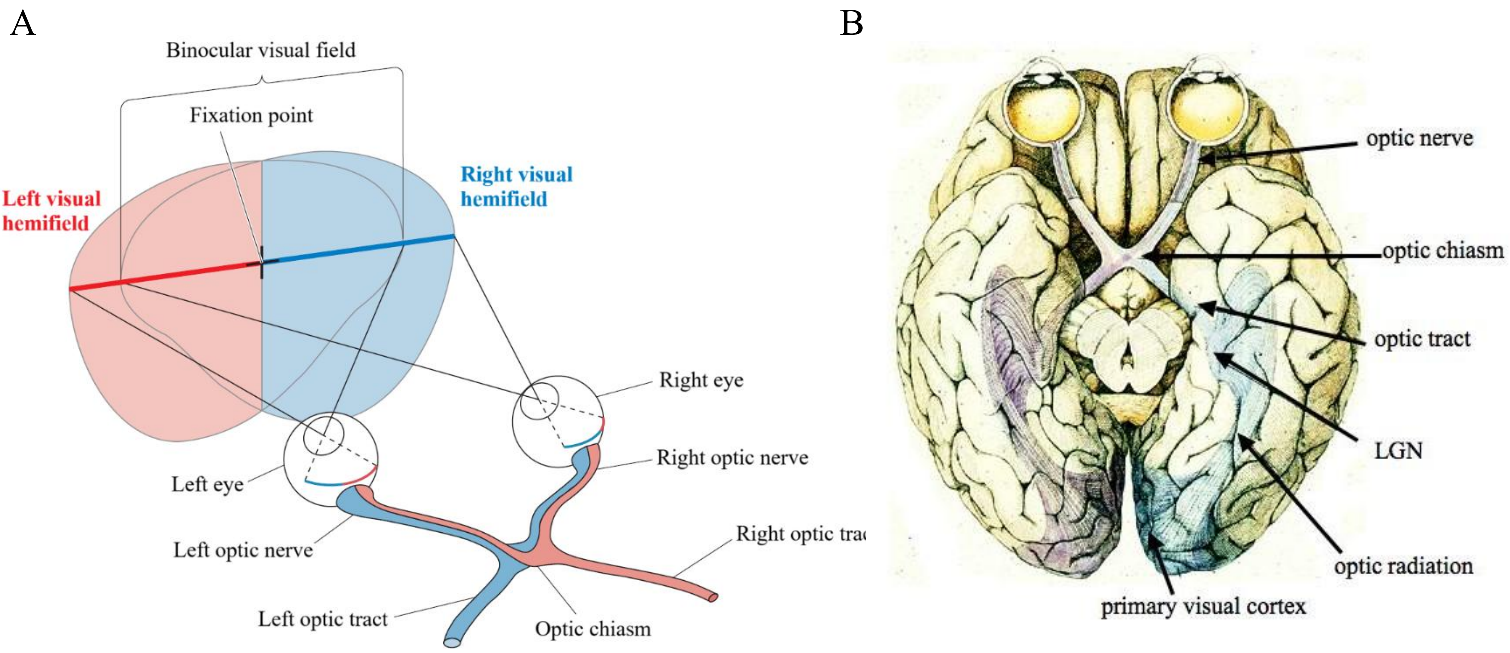

Figure 1. (A) Illustration of the retinofugal projection up to the optic tract (adapted from Bear et al., 2007) and (B) ventral view of the retinogeniculate visual pathway from the retina to V1 (adapted from Hubel, 1988).

pigmented epithelium to minimize reflection. There are two types of photoreceptors: cones and rods. Cones have shorter outer segments containing fewer photopigment membranous disks, while rods have longer outer segments and contain more disks. The main difference between cones and rods is that rods are more sensitive to light and have only one type of photopigment, thus allowing vision in low-light conditions, while cones contain photopigments sensitive to specific wavelengths (560 nm i.e. red, 530 nm i.e. green and 420 nm i.e. blue) and are less sensitive to light, allowing high-definition coloured daylight vision. Photoreceptors transduce light energy into changes in membrane potential, making it possible for visual information to travel from the photoreceptors to bipolar cells and then to ganglion cells, the axons of which pass through the optic disk, creating the blind spot and forming the optic nerve. The optic nerves from both eyes then merge at the optic chiasm, where most fibres from the nasal retinas cross to the other side (i.e. decussation). Thus, axons from the right temporal and the left nasal retina form the right optic tract which carries information from the left visual hemifield towards the right V1, and vice versa (see Fig. 1 for illustration). Most of the axons of the optic tract form connections in the LGN (lateral geniculate nucleus). From here, neurons give rise to the projection towards the primary visual cortex (V1) called the optic radiation.

The retina is not the main source of input to the LGN. Most of its input is from V1, even though the function of this input is still unclear. The LGN also receives input from neurons in the brain stem. This intricate network is known as the corticofugal feedback pathway. Therefore, the LGN seems more than a simple relay from retina to cortex; it is the first site in the ascending visual pathway where what we see is influenced by how we feel (Bear et al., 2007).

1.1.2 V1

The primary visual cortex (V1), or striate cortex, – Brodmann's Area 17 – is located in the occipital lobe. As seen above, it is the final projection of the corticofugal pathway, and is the first of several visual cortical areas.

A key organizational feature present throughout the visual system is called retinotopy: it means that neighbouring cells in the retina project to neighbouring locations in the target structures, thus mapping the surface of the retina onto the surface of the target structures. This organizational feature has specific characteristics. First, the representation of the visual field is distorted in the striate cortex: the central few degrees of the visual field are magnified in the retinotopic map. Second, when the retina is stimulated by a point of light, the activity in the striate cortex takes the form of a broad distribution with a peak at the corresponding retinotopic location, due to overlap of receptive fields of the neurons.

V1 is called striate cortex because it is subdivided into discrete layers. These layers are traditionally six, but from recent studies more layers were discovered. However, it was decided to keep the original numbering, and thus subdivide layer IV into IVA, IVB, IVCα and IVCβ. Most neurons superficial to IVC have binocular receptive fields, while most neurons outside IVC are orientation selective (OS), which is an important feature for analysis of object shape. These OS neurons together form orientation columns within which neurons have the same preferred orientation across different layers. Along the horizontal, the orientation preference shifts to other degrees. There are also neurons which are direction-selective (DS) and are a subset of OS cells. DS cells fire when a stimulus is at the optimal orientation and moves perpendicular to the orientation in one direction, but do not fire if it moves in the opposite direction.

Given the retinotopic structure of the visual system, all thousands of neurons processing a point of visual space are located in a circumscribed patch of V1. This has been called a cortical module. A cortical module is a 2x2 mm chunk of cortex containing two complete sets of ocular dominance columns (16 blobs) and, in the cells between blobs, a complete sampling of all 180° of possible orientations. This is both necessary and sufficient to analyse the image of a point in space. The striate cortex contains 1000 cortical modules.

1.1.3 Other cortices (extrastriate areas)

The dorsal stream (from V1 towards the parietal lobe) appears to serve the analysis of visual motion and the visual control of action. The ventral stream (from V1 towards the temporal lobe) is thought to be involved in the perception of the visual world and the recognition of objects.

The dorsal stream begins in V1, passes through V2 and V3, and MT/V5, before reaching PPC. It does not appear to be organized in a strict serial hierarchy, but there is a clear progression towards more complex or specialized visual representations. Area MT/V5 is specialized in object motion processing. Similarly, the ventral stream's path starts in V1, passes through V2, V3, V4, and IT before reaching the temporal lobe. Area seems to be specialized for shape and colour perception. Area IT has a complex role: it is important for both visual perception and visual memory, and also a small percentage of its neurons strongly responds to faces. The receptive fields of the cells in the higher visual areas are enlarged – and more complex – and this is a clear trend throughout the visual brain. Such enlargement is due to convergent anatomical input from V1 and local connections that refine the substructures of the receptive fields (Zeki, 2015). All mid-tier visual areas, including V5, receive two sets of parallel input:

one set of input comes from more than one antecedent cortical visual area and the other one from the cortex and sub-cortex (e.g. LGN) (Shigihara & Zeki, 2014). ffytche et al. (1995) named such information flow *dynamic parallelism*, from the evidence that subcortical areas send simultaneous parallel inputs to V1 and extrastriate areas, but whether both pieces of information become active at the same time depends on the specific characteristics of the stimuli (i.e. fast motion is preferred by V5, hence it would be activated earlier by a fast stimulus compared to V1). An interesting consequence is that V1, according to Zeki, is not necessary for conscious perception of visual stimuli, because conscious perception can be achieved also when V1 is lesioned, as studies in the 90s on blindsight suggest (Barbur et al., 1993). It is even more interesting to note that this is not a novel discovery, because even George Riddoch in 1917 described (impoverished) conscious perception of (fast and high contrast) moving stimuli in V1-lesioned patients, but these results were ignored up until the 90s (Zeki, 2015).

Regarding more specifically V5, its neurons have large receptive fields that respond to stimulus movement in a narrow range of directions (most of the cells are direction-selective (DS), i.e. about 90%). Since neighbouring neurons tend to be tuned to similar stimulus parameters (Riečanský, 2004), V5 is arranged into direction-of-motion columns analogous to the orientation columns in V1. V5 neurons are particularly sensitive to fast motion, while slow motion is more related to activity in DS cells in V1. Furthermore, they lack colour sensitivity but are highly sensitive to luminance. Presumably, the perception of movement at any point in space depends on a comparison of the activity across columns spanning a full 360º range of preferred directions (Bear et al., 2007). Lesions, magnetic and electric stimulation of MT/V5-complex impair movement perception (akinetopsia) and deficits are more severe when adjacent areas are damaged (i.e., MST, Medial Superior Temporal), for example impairments in initiation and maintenance of smooth-pursuit eye movements (Riečanský, 2004). Moreover, MT/V5+ seems to be related to high-order motion (e.g. it is activated by illusory motion, implied motion, mental imagery of motion, motion in other modalities). More specifically, in the perception of implied motion, the activity of MT/MST seems to be modulated by other areas in a top-down fashion (Kourtzi & Kanwisher, 2000). This is relevant in the perception of Representational Momentum, as will be discussed in the later section.

Another area critical to motion perception is MST, which contains cells selective for linear motion (as in MT), radial motion (either inward or outward from a central point), and circular motion (either clockwise or counterclockwise).

1.2 Representational Momentum

1.2.1 Definition and findings

Representational Momentum (RM) is a cognitive phenomenon in which the judged position of a moving stimulus is displaced in the direction of anticipated motion (Hubbard, 2014). This is in line with the general belief that the brain tries to predict the outcome of events and stimuli. RM was first described by Freyd and Finke (1984). Since then, numerous articles and experiment were carried out to better understand this phenomenon, but a general theory is yet to be formulated. Advocates of a high-order description suggest that RM reflects the actual momentum of the representation, meaning that the representation shifts in position as real-world objects affected by momentum do. However, also low-level explanations have been proposed. I will discuss theories and models in a later section.

The term "representational momentum" has been used in a broader sense to refer to any displacement of the position of a moving object in the direction of motion. However, this usage can be theoretically misleading. Therefore, Hubbard (2005, 2010) proposed a narrower sense to be used to refer only to the displacement that reflects internalized momentum. Moreover, Hubbard highlighted that "representational momentum" was utilized to refer both to the displacement and the mechanism behind it, but it would be clearer to simply use "displacement" to refer to the displacement.

A typical experiment studying RM involves the presentation of a set of computer-generated smoothly moving stimuli (e.g. a bar rotating, a probe moving along a horizontal line, etc.) or a set of implied motion stimuli (i.e. spatially and temporally discrete snapshots that imply motion in a certain direction; for illustration of a typical procedure see Fig. 2). After the target has travelled a specific distance (or a specific number of snapshots has been presented), it vanishes; then a probe may appear in the same location, slightly forward or backward and the participant has to judge whether the probe appeared in the same or a different location compared to the orientation of the last inducing stimulus. If motion is consistent, meaning that all inducing stimuli come one after another in a way similar to real motion, participants are more likely to respond *same* to probes presented slightly forward than to probes presented slightly backward. For clarification, no actual continuous motion is possible with computer-generated stimuli, since there will always be even the tiniest latency between frames. When talking about continuous motion, I am referring to the perception of continuous motion by the participant and this is possible because the SOA (stimulus onset asynchrony) between successive target presentations is very small.

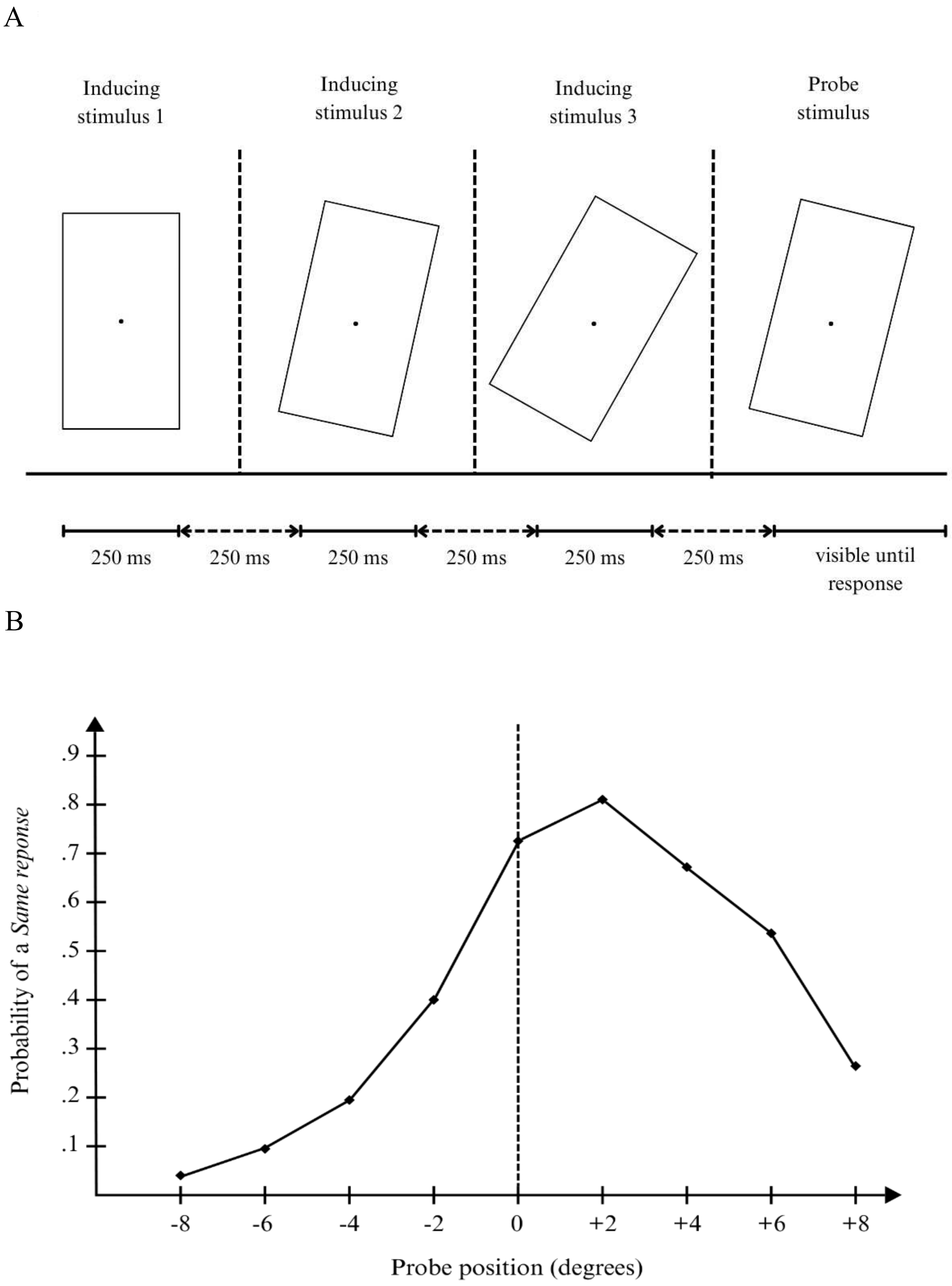

Figure 2. (A) Experiment methodology using implied motion stimuli and (B) results adapted from Freyd and Finke (1984).

Other forms of RM include Representational Gravity (i.e. displacement along the vertical axis; RM and RG combine for descending targets, while they cancel out for ascending ones; Hubbard, 1995), Representational Friction and Representational Centripetal Force (Hubbard, 2005). Hubbard (2014), in his review, suggested the existence of other types of momentum: Attentional and Operational Momentum. Attentional Momentum describes that a shift in the direction of movement of attention requires first to overcome the momentum in the current direction of movement. Operational Momentum describes the phenomenon in which one overestimates sums in additions and underestimates differences in subtraction. However, Hubbard highlights that it is still under debate whether Attentional Momentum and Operational Momentum are separate phenomena or can be described as subtypes or particular manifestations of RM.

Among the characteristics of the target that influence displacement, the most well-established effects are target velocity and acceleration, meaning that an increase in velocity or acceleration produces and increase in forward displacement. On the other hand, it is not observed a consistent forward displacement for either rightward or leftward motion nor for either clockwise or counterclockwise motion. Target size and implied weight influence displacement only along the vertical axis, thus this can be attributed to RG. RM occurs also with different types of stimuli. For example, the human face can be used as a stimulus and the velocity in change of facial expression (from neutral to emotional expression) can be manipulated: in Yoshikawa and Sato's (2008) work they observed that participants' responses reflected a more extreme expression than the one of the target, and the extremity of expression positively correlated with the velocity of change in facial expression. Finally, RM may occur in different modalities, such as acoustic modality (Johnston & Jones, 2006), or crossmodally (Hubbard & Courtney, 2010).

RM occurs with continuous motion, implied motion and frozen-action photographs[1]; this has crucial theoretical relevance because it demonstrates that for RM to occur eye movements are not necessary (Hubbard, 2005), but may still pose an influence. For example, in tasks where continuous motion is used, constraining eye movements (i.e. not allowing the smooth pursuit of the target) has a drastic effect on displacement, significantly reducing it (Kerzel, 2003). Conversely, if a motor response is requested, meaning that instead of judging the location of a probe compared to the target the participant has to directly point to the vanishing location of

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[1] Frozen-action photographs are images or video frames taken from a longer motion sequence.

the target, constraining eye movements has little effect, and displacement is still observed (Kerzel & Gegenfurtner, 2003).

Furthermore, it is thought that the retention interval plays an important role, since displacement decreases if the latency between the last inducing stimulus offset and the probe onset exceeds 500 ms (Hubbard, 2005); but this is not the case for RG, as downward displacement increases up to 1200 ms of retention interval (De Sá Teixeira et al., 2013). It also seems that if less attention is allocated to the task, an increase in forward displacement is observed. Alternatively, if attention is divided between the target and another stimulus, forward displacement increases; "It may be that a division of attention results in larger displacement while a target is visible, but once the target vanishes, the representation of the target is more fragile and a perceived distractor masks any forward extrapolation of the target that would otherwise have occurred." (Hubbard, 2005, p. 18). However, the reverse might also be true, meaning that displacement may influence the allocation of attention.

Finally, it is interesting to note that knowledge about RM influences displacement, meaning that if a participant is instructed on the workings of RM, less forward displacement occurs than in naïve participants (Courtney & Hubbard, 2008).

1.2.2 The role of cortical areas

Even though RM is clearly observed in behavioural studies and there is large a large body of literature on the topic, cortical areas or networks that modulate the phenomenon are yet to be universally identified. Interestingly, there seem to be an anatomo-functional dissociation between RG and RM, meaning that the temporo-parietal junction (TPJ) seems more related to RG and hMT/V5+ to RM. For example, as opposed to RM (see above), constraining eye movements appears to have little effect on displacement in RG tasks (De Sá Teixeira et al., 2019). The importance of area MT/V5 for representational momentum was also illustrated by an absence of displacement if a task previously shown to elicit it was performed immediately after transcranial magnetic stimulation (TMS) of area V5/MT (De Sá Teixeira et al., 2019). But this claim is far from conclusive, since Rao et al. (2004) reported no increase in activity in hMT/V5+ using fMRI when participants were asked to provide perceptual judgment to implied motion stimuli, while the observed RM effect was robust. They used Freyd and Finke's (1984) design, thus both RM and control condition used implied (discrete) motion stimuli. An explanation Rao et al. gave for the reason no difference in activity in MT was found was that MT could have no actual role in RM, but it might instead underlie the perception of implicit motion. Conversely, they detected increased activity in PFC (prefrontal cortex). They suggested an explanation regarding working memory: given that a fronto-parietal network may be involved in working memory processes and that such processes may be required in the RM effect, it may be that the observed effect reflects the coherence of the inducing stimuli represented in working memory. To add to this, De Sá Teixeira et al. (2019) noted that only studies which used static images with implicit motion as stimuli reported an increase in activity in hMT/V5+ (see Senior et al., 2002 for TMS study).

1.2.3 Explaining RM

Just as not all changes in or forces acting upon physical objects involve physical momentum, not all displacement involves representational momentum (Hubbard, 2005). Implied physical principles can influence displacement, but RM is not simply an internalization of physical momentum because non-physical variables also have an impact on displacement. For example, knowledge about target identity and subsequent expectations regarding its possible motion, attribution about causality of target motion and many other higher-order variables influence displacement (Hubbard, 2010). It is relevant to highlight that physical laws and people's ideas about such laws (i.e. naïve physics) do not always match (Kozhevnikov & Hegarty, 2001).

Of interest, most of the effects described above were elicited by extremely simple computer-generated stimuli, which obviously are not subjected to physical principles such as momentum of gravity. This shows how strong the biases of representation of physical properties actually are (Hubbard, 2005).

RM is thought to be relevant to object localization and motor responses in everyday tasks, since we live in a world that is in constant motion. For example, its role in spatial localization of stimuli is crucial because it serves the function of filling the gap between perception and action (Hubbard, 2005). When we detect a moving target, the brain must first process the perceptual information, then higher-level mechanisms further process the data, and only then can a motor response start. Such processes take time – even though it is on the order of a few milliseconds – and before the motor response takes place, the target would have already continued to move. Therefore, the most effective response to the target would be the one that considers the position of the target when it will be reached by the effector (i.e. hand), not the location when the first processes began.

There is not a general theory that can explain RM and displacement thoroughly, but several theories have been proposed that explain specific aspects of RM. According to Hubbard's (2010) classification, theories can be divided into (a) internalization theories, (b) belief-based theories, (c) neointernalization theories, (d) low-level theories, and (e) network models. These approaches can be very specific and can explain only parts of the available data, therefore they will not be discussed here.

There are currently attempts at creating a unified view of RM, which can be summed up in two main approaches: Kerzel's (2005; 2006) bottom-up three-factor approach and Hubbard's top-down computational theory of RM (Hubbard, 2006).

According to Kerzel, there are three factors that influence forward displacement: eye movements (present or absent), response type (verbal or motoric) and motion type (continuous or implied). Kerzel suggests that forward displacement is caused by eye movements pursuing a smoothly moving target that continue on because they cannot be halted immediately after the target has vanished. Thus, displacement is produced by a motor response rather than a verbal (symbolic) one. In this approach, no internalization of physical principles is hypothesized and hence the mechanisms producing displacement are of perceptual or motoric nature. This approach explains some of the data regarding displacement, but does not address displacement that occurs in implied motion stimuli or frozen-action photographs.

According to Hubbard, a computational theory would be more suited to explaining RM. A computational theory of a process addresses first its function and benefits for the survival of the organism that takes advantage of it (Marr, 1982). For example, displacement could aid in the spatial localization of stimuli and navigation in the environment. Moreover, a computational approach prefers to look at the process through a wider lens addressing constraints of the information being computed, thus it does not consider the specific mechanism regarding computation right away (Hubbard, 2005). However, such a computational theory is yet to be thoroughly formulated.

1.3 Neural oscillations and EEG

Rhythmicity is ubiquitous in the physical world; for example, day-night and season cycles impose a great influence on living organisms, but since they grew and developed in this world, organisms evolved strategies and mechanisms that facilitate living along these rhythms, for example wake-sleep cycles and difference of behaviours across the seasons. In addition, sensory processes appear to be cyclic, meaning that there is evidence that animals sense the environment in snapshots.

Synchronous activity is characterized by frequency (Hz) and amplitude (μV). Different names were given to such activity: brain waves, neural oscillations, brain rhythms; I will use these terms interchangeably. The rhythms are categorized by their frequency range. *Gamma rhythms* (>30 Hz) are involved in high-level cognitive functions like attention and memory. *Beta* *rhythms* (13-30 Hz) are associated with sensorimotor processing and signal an activated cortex. *Alpha rhythms* (8–12 Hz) are associated with quiet, waking states and seem to have an integrative function in perception. *Theta rhythms (*4–7 Hz) occur during some sleep states. *Delta rhythms* (<4 Hz) are often large in amplitude and are a hallmark of deep sleep. Low-frequency, high-amplitude rhythms are associated with nondreaming sleep states. This is because processing information, whether generated by sensory input or by internal processes, requires single or small groups of cortical neurons to be highly involved in specific tasks but also relatively unsynchronized. This leads to low EEG amplitude and high frequency. By contrast, during deep sleep, neurons are not engaged in information processing, and a large number is excited by a common, low-frequency rhythmic input. In this case synchrony is high, so EEG amplitude is high.

Neural oscillations can be generated by a pacemaker, e.g. thalamic neurons, by spontaneous mutual inhibition and excitation between neurons, or by a combination of both.

The electroencephalogram (EEG) is one of several instruments used to measure neural activity. It was first described by Berger in 1929. It is an instrument that enables measurement of electricity generated by synaptic excitation of the dendrites of many pyramidal neurons in the cerebral cortex. It works by applying metal electrodes touching the scalp, often via a conducting gel that helps reducing electrical impedance. There are standard, fixed positions of electrodes on the scalp. The EEG signal is usually in the order of magnitude of tens of microvolts (μV) in amplitude and is the result of differences in voltages between a given pair of electrodes. It is not a surprise that the electrical contribution of any single cortical neuron is minuscule, moreover the signal must penetrate several layers of non-neural tissue (meninges, fluid, bones, and skin) to reach the electrodes; therefore, the synchronous activity of thousands of neurons is necessary to generate a signal large enough to be detected. It is interesting to note that, when each cell receives the same amount of excitation, but spread out in time, the summed signals are meagre and irregular. Thus, the key for brain waves is synchronicity over time.

Communication Through Coherence (CTC) hypothesis (Fries, 2005, 2015) proposes that phase-locking (i.e. synchronization) of oscillations between neuronal groups facilitates or inhibits communication. This hypothesis is supported by the fact that activate neuronal groups have the intrinsic property to oscillate (Buzsáki & Draguhn, 2004) and that oscillations reflect levels of neuronal excitability, affecting spike output and sensitivity to synaptic input. If two groups of neurons are synchronized, communication between them is more effective because output and input windows are available at the same time.

1.3.1 The role of beta-band oscillations

Even though there is no unified view of the roles of neuronal oscillations, there is correlational and causal (i.e. from brain stimulation) evidence of their functions in visual tasks (Battaglini et al., 2020; Di Dona et al., 2024). For example, beta-band activity (BBA) seems to be related to motor processes and the perception of motion. It has been suggested that beta oscillations are the predominant rhythm in parietal areas and supports visual processing through the dorsal stream (Di Dona & Ronconi, 2023). In addition and more specifically, BBA appears to serve to the maintenance of the current cognitive and motor set (Engel & Fries, 2010). According to Engel and Fries's, it seems that BBA is increased if a strong top-down endogenous control is needed in a cognitive task, while if a task requires stimulus-driven decisions, BBA is decreased. Moreover, BBA seems to have a notable function of interareal communication through neural synchronization (Fries, 2015).

1.4 tACS and neuronal entrainment

Entrainment is defined as the alignment of one or more oscillating systems to an external rhythm, whereby the interaction is unilateral (Lakatos et al., 2019). A bidirectional relationship between two oscillators is called synchronization and is thought to reflect network activity. Entrainment enables or disables communication between two systems through aligning the recipient's activity with the sender's activity at specific phase delays. Thus it can facilitate communication between perception and production (motor) areas in the brain (active sensing). Active sensing is a process in which the (voluntary) rhythmic motor activity patterns entrain neuronal oscillations in sensory brain regions; this means that the motor system "informs" the brain that a sensory input is coming with a specific delay. The delay is thought to be conveyed by a phase shift that corresponds to such latency. Moreover, the brain can align brain oscillations to the temporal structure of inputs to facilitate their processing, whether they are in themselves rhythmic or the sampling of the environment is.

In Lakatos et al.'s (2019) review, they distinguish between environmental rhythms (external and sensory); self-produced rhythms (voluntary motor ones and involuntary autonomous ones); and rhythmic neuromodulation (tACS and other oscillatory types of stimulation).

Transcranial alternating current stimulation (tACS) has the capability to better illustrate the causal link between brain waves and perception. There is evidence that tACS constitutes an efficient method to significantly entrain the brain's cortical oscillations during and after the stimulation (Helfrich et al., 2014). However, tACS and other forms of neuromodulation produce peripheral sensations in the recipient, therefore have to be sham-controlled in experimental settings, meaning that a placebo-type stimulation has to be administered to the participants. Moreover, in order to exclude that an observed behavioural effect is due to the mere fact that the brain receives electrical stimulation, and instead assess a band-specific effect on behaviour, participants must be stimulated within at least two different bands (e.g. within the beta band and the theta band, as it will be illustrated in the current study). All these peculiarities often require that the participant takes part to several experimental sessions, possibly leading to fatigue, practice effects related to the task, and reluctance to volunteer to the study or to continue participating (drop-out).

As highlighted above, the role of brain stimulation is crucial in experimental psychology, because it can assess the causal relationship between different phenomena. However, in order to understand whether brain oscillations can be entrained by tACS, it is necessary to utilize simultaneous electrophysiological recordings of brain activity (e.g. EEG) (Helfrich et al., 2014).

1.5 Current study hypotheses and expected results

As readers may have noticed, I have not mentioned any study regarding a relationship between RM and beta oscillations; this is because such studies are yet to be published. Di Dona et al. (*in preparation*) have gathered EEG correlational data regarding the above-mentioned relationship. More specifically, they used the same RM task and stimuli as the current study's (see 2.2 and 2.3); they found that when the probe bar was tilted slightly forward and the participants were more likely to respond *equal*, a difference in beta power and beta frequency was observed such that *equal* > *different*. While, if the probe was tilted backwards such difference was not observed. Therefore, given this crucial and novel finding and the evidence reviewed above, we decided to test this relationship with a causal paradigm. Specifically, we believe that the dorsal stream, PPC and BBA are coupled in the perception of motion.

In the current study, we had participants performing an RM task on a computer in which a bar rotated smoothly following a clockwise path. While the participants were performing the task, we administered tACS in the beta (17 Hz) and theta (6 Hz) bands, in addition to a sham (placebo) condition, in a bilateral parietal layout (see Fig. 3 and 4, hence targeting PPC and, because high definition tACS is not as focal as, for example, TMS, also V5/MT was targeted). While stimulating at 17 Hz, we hoped to see entrainment of neurons in those areas and a boost in beta power and frequency, thus we expected to see a cancellation of the RM effect, while no effect should be observed in the theta and sham conditions. This is because the differences in beta power and frequency are little and should be easy to influence.

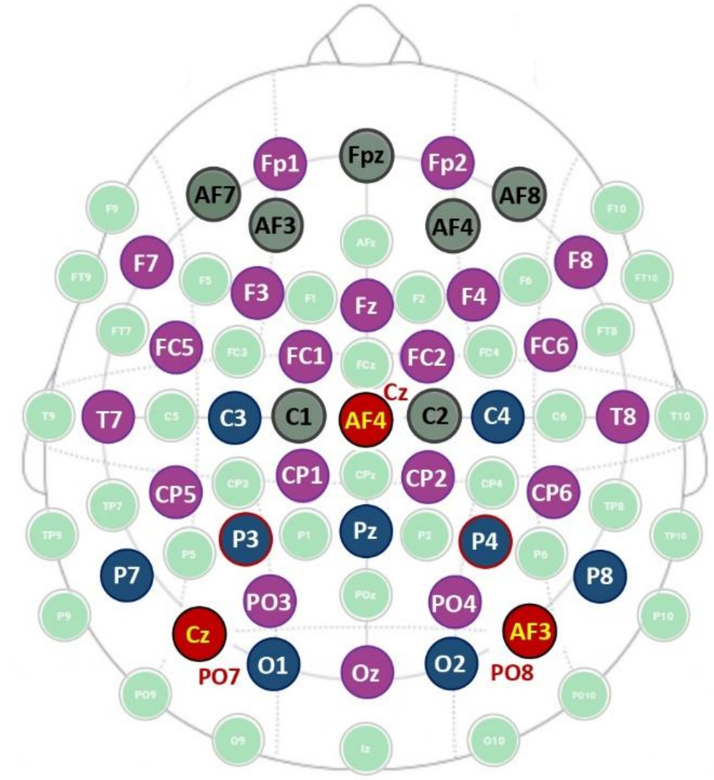

Figure 3. Bilateral Parietal EEG-tACS stimulation layout. Purple and Red circles indicate EEG recording electrodes, while blue circles indicate stimulation electrodes (P3 and P4 are source electrodes, and the others return electrodes).

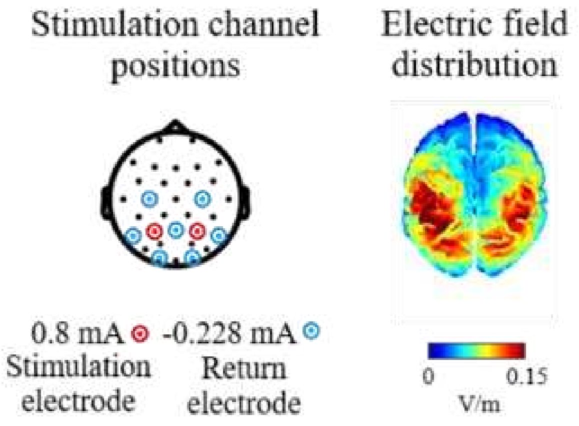

Figure 4. The location of the stimulation, intensity and electric field distribution.

Chapter 2 – Materials and methods

2.1 Participants

The sample was calculated to be of 30 people. Each person was to be subjected to three experimental sessions for a total of $30 * 3 = 90$ sessions. Unfortunately, at the start of data collection the EEG-tACS device underwent maintenance because we detected artifacts in the EEG signal that would have compromised the quality of the recording. Therefore, we only tested 10 participants, two of which completed only two sessions and one of which was subject to only one session. Because of this, the analyses will have significantly less statistical power, and we will be extremely cautious at drawing conclusions from the collected data.

All ten participants (5 F, Age = 21.6 ± 2) were students at the University of Padova. All had normal or corrected-to-normal vision, were right-handed and were naïve to the objectives of the study.

All participants fell withing the criteria of tACS administration (Antal et al., 2017), which were checked using a questionnaire (see Supplementary Materials). In addition, we let them fill a questionnaire about sensations arisen from stimulation (see Fertonani et al., 2015) at the end of each session.

The study was approved by the Ethics Committee of the Department of General Psychology of the University of Padua (prot. nr. 1104-b). Research followed Helsinki Declaration principles. Before testing, participants signed an inform consent.

2.2 Stimuli, task and apparatus

The stimuli were displayed binocularly on an Asus ROG Swift OLED PG27AQDM monitor with a diagonal of 26.5” and refresh rate of 240 Hz. Display resolution was of 2560 × 1440 pixels. Participants were seated at a mean distance of 57 cm from the screen, and their head was kept in place by a chin holder.

In the RM task (see Fig. 5 and 6 for illustration), a white fixation dot appeared at the centre of the screen for 750 ± 250 ms (jittered) in a dark grey background (RGB). Next, the “inducer” bar (length = 8 deg; width = 1.34 deg, light grey RGB), appeared at the centre of the screen and rotated clockwise at three possible speeds (50, 70 or 90 °/s) for 1000 ms before disappearing. After a blank of 250 ms the “probe” bar was presented for 1000 ms and could appear either in the same orientation of the inducer bar before its disappearance (rotation 0°) or slightly tilted clockwise or counterclockwise (offsets: ±1°, ±2°, ±3°, ±4°, ±5°; see Fig. 6).

Participants were instructed to report if the probe had the same or different orientation with respect to the final position of the target using the “M” and “Z” keys on the keyboard (response mapping was counterbalanced across participants). Participants performed 20 practice trials before starting the experimental task which was composed of 4 blocks of 165 trials each (660 in total, ≃ 40 minutes) with small breaks in between the blocks. The experiment was run using MATLAB (The MathWorks Inc., 2021) PsychToolbox (Kleiner et al., 2007).

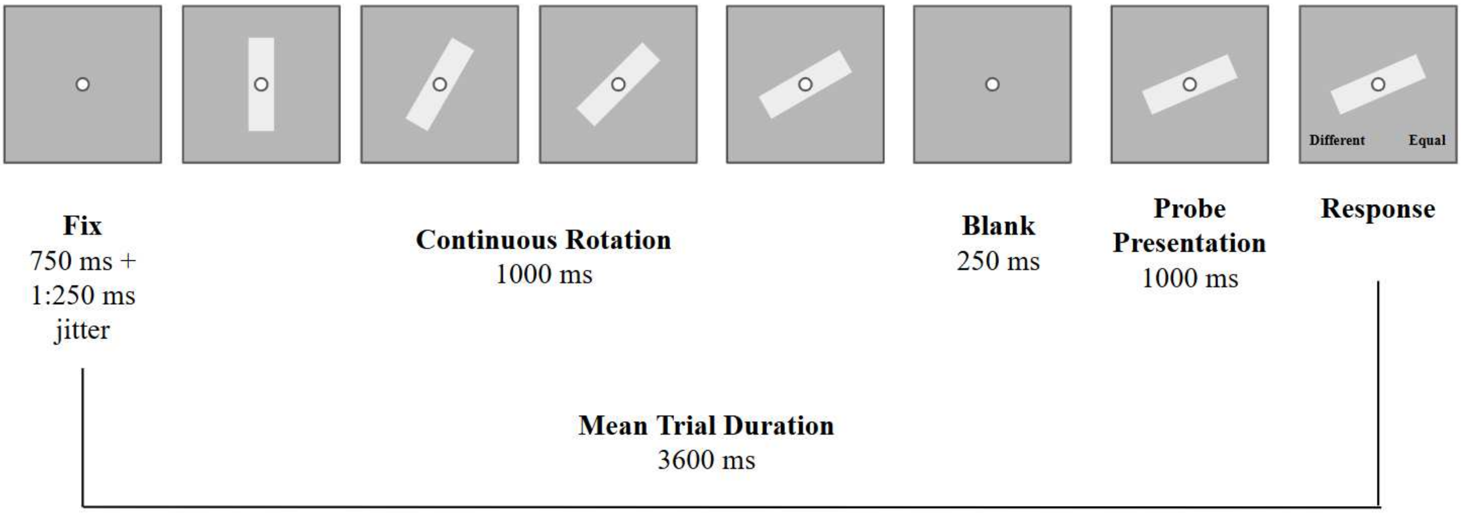

Figure 5. Illustration of the RM task.

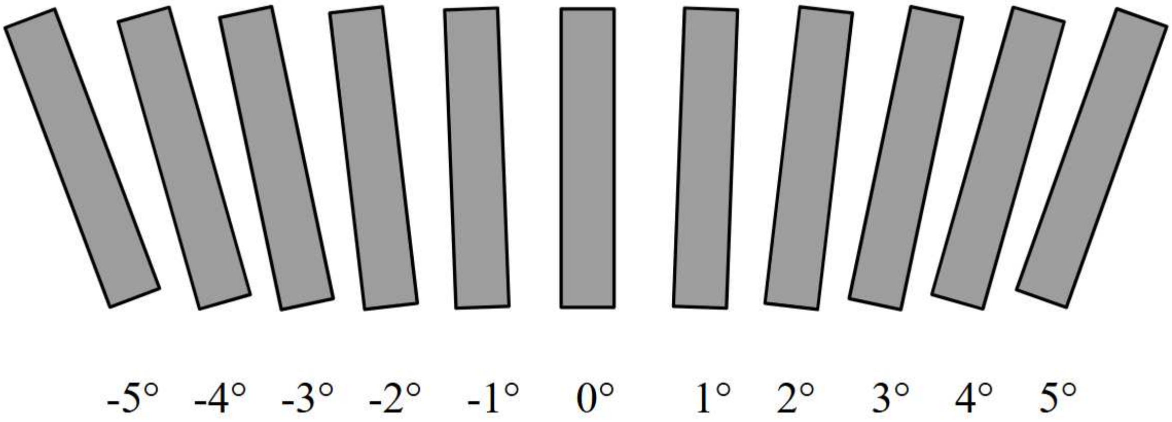

Figure 6. The eleven different offsets of the probe bar.

2.3 Procedure

We implemented a within-subject design in which each participant took part in three tACS sessions in three different non-consecutive days. On every session, while the participant was performing the RM task, a different tACS protocol could be administered: within the theta band (6 Hz), the beta band (17 Hz) or sham (control) condition. The precise stimulation frequency

(17 Hz) was chosen based on a previous EEG study (Di Dona et al., *in preparation*) in which it exhibited the maximum power modulation when the RM effect was present. The order of the three sessions was counterbalanced between participants. Each session took place in a dimly light room and consisted of: the participant read and signed the informed consent and filled the exclusion criteria questionnaire (Antal et al., 2017); then, we mounted the tACS/EEG apparatus which took on average 20 minutes; later, we recorded 4 min. of pre-stimulation resting-state EEG; then, the participant performed the RM task while receiving 41 min. of stimulation; finally, 4 min. of post-stimulation resting-state EEG was recorded. After the session concluded, the participant filled a questionnaire related to sensations arisen from the stimulation (Fertonani et al., 2015). The participant was instructed to move as little as possible and to keep the eyes closed during EEG recording. The participants were not aware of the stimulation conditions.

The reason for the pre- and post-stimulation EEG recording is to observe the effect of the electrical stimulation on endogenous brain activity, but such data will not be analysed in the present work.

2.4 tACS stimulation setting

The electrical stimulation was administered through the 32-channel hybrid device Starstim and NIC2 software from Neuroelectrics[2], allowing simultaneous stimulation and EEG recording. Participants wore a neoprene headcap with wholes corresponding to the international 10-20 EEG system. After gently scrubbing the scalp using a blunt needle and applying Neurogel for lowering impedance, PISTIM Ag/AgCl electrodes were mounted in the holes following the stimulation protocol (see Fig. 3 and 4). Stimulation electrodes (blue) were mounted on P3 and P4, while return electrodes were mounted on C3, C4, Pz, P7, P8, O1 and O2 locations (1 cm radius); while EEG recording electrodes (purple and red) were mounted on Fp1, Fp2, Fz, F3, F4, F7, F8, FC1, FC2, FC5, FC6, Cz, CP1, CP2, CP5, CP6, T7, T8, PO3, PO4, PO7, PO8 and Oz locations. Cz, PO7 and PO8 electrodes were attached to AF4, Cz, and AF3 cables, respectively. This was done for practical reasons because of cable length. We used this stimulation setting to target PPC and the dorsal stream, but also V5/MT was probably targeted because the device we used is not as focal as, for example, TMS.

The peak-to-baseline intensity of the stimulating electrodes was set at 0.8 mA with 0° phase, while the intensity of return electrodes was put to 0.228 mA with 180° phase. Stimulation intensity was chosen following the tACS safety guidelines (Antal et al., 2017). The total dosage

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[2] https://www.neuroelectrics.com/starstim-32

of Beta-tACS and Theta-tACS protocols was 2749.2 mC (microCoulomb) for 40 min of stimulation. In the sham protocol, 17 Hz or 6Hz tACS stimulation was delivered only for 30s at the beginning and at the end of the task with ramped-up/down intensity.

For the first four participants, a reference electrode was applied to the right earlobe after scrubbing the skin with ethylic alcohol. However, after noticing the artifacts on the EEG signal mentioned above (see 2.1), we thought that they would be reduced if we used a different kind of reference electrode. We opted for ECG electrodes applied on the mastoid. Therefore, participants 5 to 10's brain activity was recorded using such electrodes as reference.

Chapter 3 – Results

3.1 Data analysis

The magnitude of the RM effect was operationalised by computing the weighted mean (WM) which is a summary measure to represent the shift of the whole response curve (see Fig. 7). First, the proportion of *same* responses for each of the eleven offsets was calculated. Next, the proportions were multiplied by their associated offset in order to get the "weight". Then the obtained scores were summed up across offsets and finally divided by the sum of the proportions across offsets. This procedure was performed in each individual participant separately by speed and condition. An RM-ANOVA was performed to analyse the effect of condition (Beta-tACS, Theta-tACS, Sham) and speed (50, 70, 90 °/s) which were imputed as within-factors. A second ANOVA was performed on the differential score of the WM (ΔWM) obtained by subtracting the WM at 50 °/s from the WM at 90°/s. This index indicates the modulation of speed of the RM in each condition. A second ANOVA was performed on the ΔWM with the within factor condition only. General accuracy was further analysed via generalised linear mixed models with the formula *Accuracy ~ Condition x speed + (1|sj)* where participants were imputed as random factors. Effects were evaluated via Chi-Square test and post-hoc were performed on the estimated marginal means of the model.

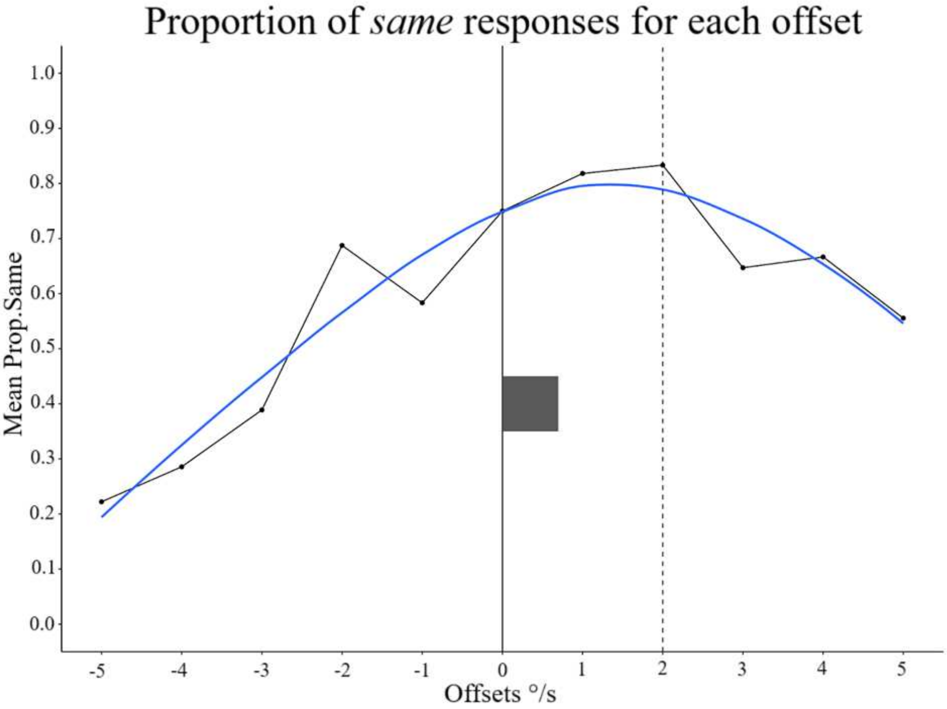

Figure 7. Plot of the weighted mean (grey bar at the centre). It illustrates the magnitude of the RM effect, which was replicated in the present study.

3.2 Results

The Anova on the WM showed no effect of speed nor condition (see Fig. 8). The Anova on the ΔWM showed no effect of condition. However, a numerical tendency was found for beta condition (M = 0.11, SD = 0.26) where the ΔWM was seemingly smaller with respect to theta (M = 0.25, SD =0.25) and sham (M = 0.24, SD =0.45) (see Fig. 9 and Table 1). The Chi-square test performed on the generalised linear mixed model showed a main effect of condition χ (2) = 39.08, p <.001. Post-hoc tests showed that when participants received beta-tACS (M = 0.36, SD = 0.15) were less accurate with respect to theta-tACS (M = 0.37, SD = 0.18; p < .001) and sham (M = 0.38, SD = 0.13, p < .001) (see Fig. 10). The remaining main effect of offset χ (1) = 15.10, p <.001, speed χ (1) = 13.58, p <.001 and the interaction between offset and speed χ (1) = 14.58, p <.001 were not analysed as not of interest for the scope of the present work.

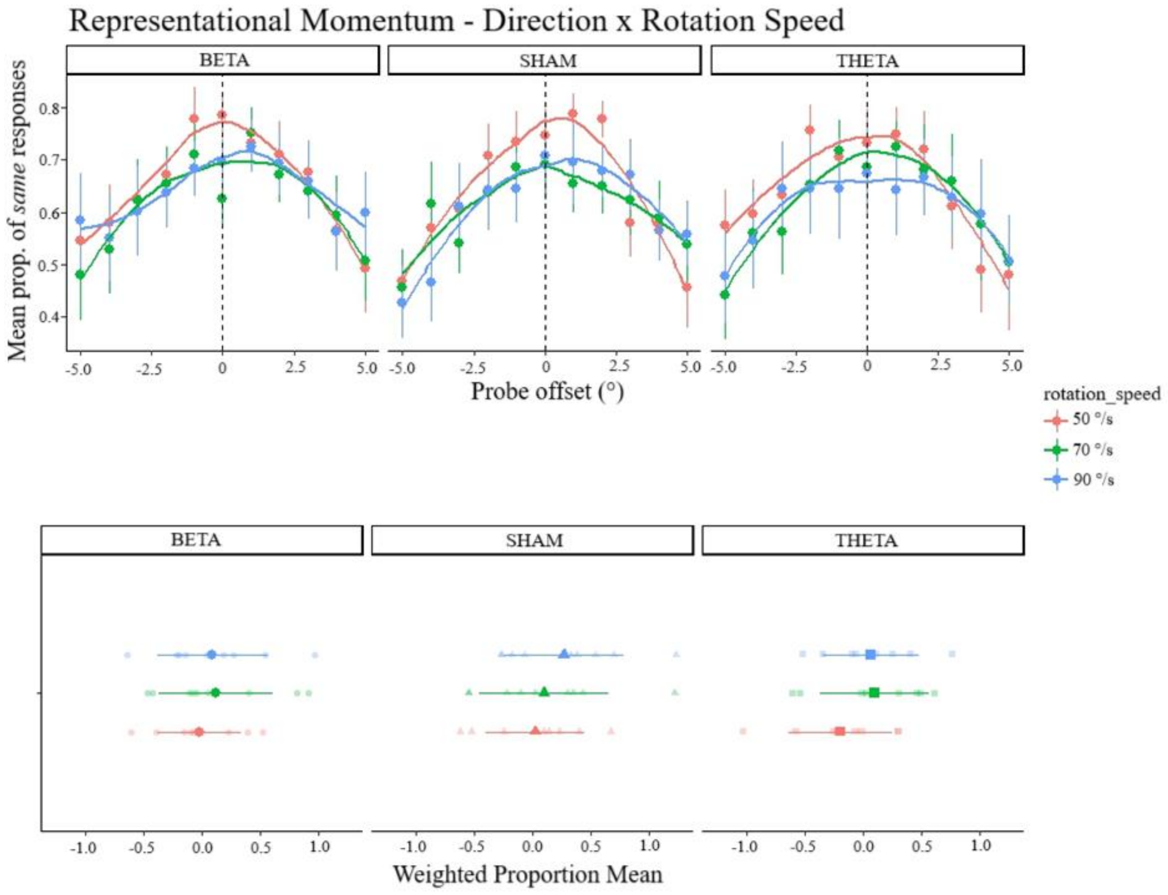

Figure 8. A plot of the results of the ANOVA on the WM which show no effect of speed nor condition.

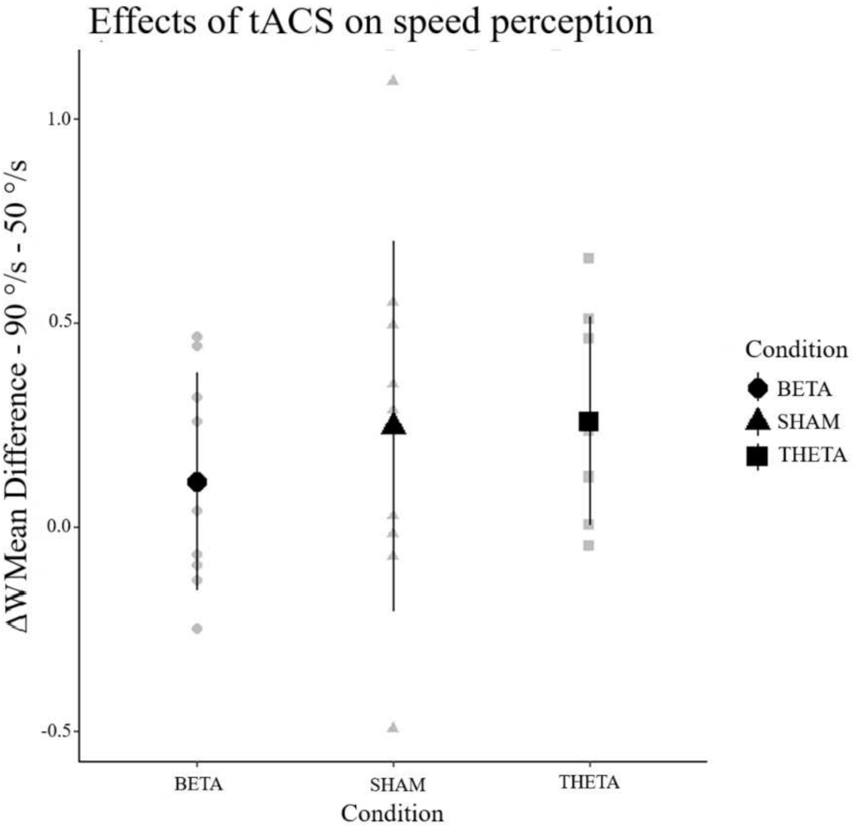

Figure 9. A plot of the results illustrated in Table 1.

	Condition		
	Beta	*Sham*	*Theta*
ΔWM 90°/s - 50°/s	0.11 ± 0.26	0.24 ± 0.45	0.25 ± 0.25

Table 1. A table of the results of the ANOVA on the ΔWM which shows no effects of tACS condition on speed perception.

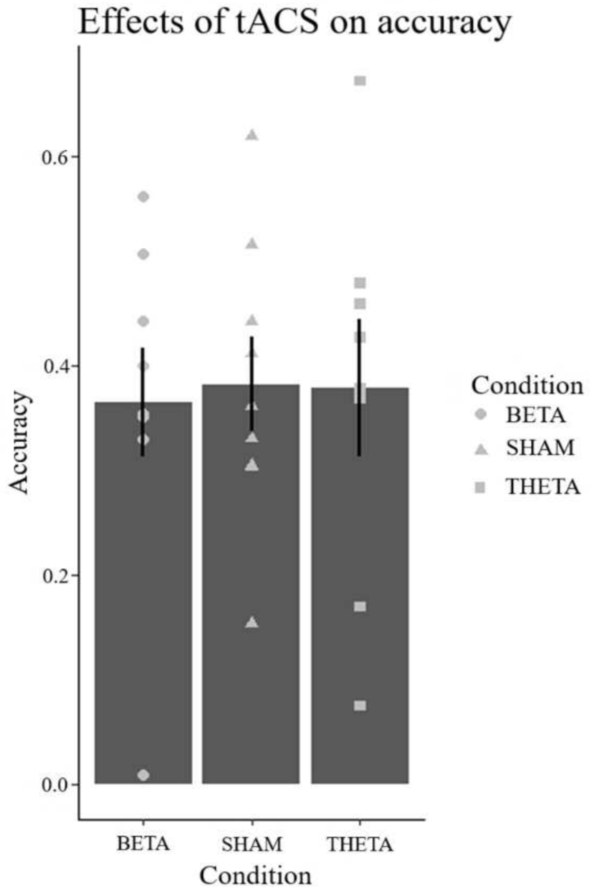

Figure 10. A plot of the results of post-hoc tests that shows an effect of condition on accuracy. Specifically, accuracy for beta-tACS is lower compared to theta-tACS and sham.

Chapter 4 – Discussion

4.1 Result summary

The present work was based on previous knowledge that tACS could entrain cortical neurons to a specific frequency in order to influence brain activity (Helfrich et al., 2014) and on the work of Di Dona et al. (*in preparation*) that observed a correlation between beta power and frequency and the tilt of the bar in the RM task. We hypothesized that an imposed beta frequency at 17 Hz (beta-tACS) on the parietal cortex could interfere in motion perception, cancelling the RM effect. Contrary to expectations, results showed no tACS-induced modulations of the RM effect and only a numerical tendency of beta-tACS in reducing the effect of speed on the task. Clearly, such results are difficult to interpret and to trust considering the high level of noise, since the sample size is way restricted with respect to the necessary one because of already mentioned issues during data collection. However, if the reduction of the speed effect on the RM were to hold robust with an appropriate sample, it would argue for a functional specificity of beta oscillations for speed perception during visual motion. In that hypothetical case, imposing a specific entraining frequency to the parietal cortex may disturb frequency-specific processes occurring within the beta band. However, these are mere speculations and cannot be inferred with the data collected in the present study.

Of interest, beta-tACS reduced the general accuracy in the task. This was not expected, because if applying tACS at beta frequency on parietal cortex should interfere with motion perception and thus lower the RM effect, a higher accuracy on the RM task would be expected. However, this is not the case. Nevertheless, such evidence can still be considered an indication of the functional specificity of beta oscillations over the parietal cortex in motion perception, but possibly pertaining to a more general mechanism of visuo-spatial perception and not necessarily motion extrapolation and prediction.

These results are also difficult to relate with any of the theoretical approaches discussed above (see 1.2.3). This is because none of the mentioned theories focus on neural oscillations nor on brain areas that could be related to RM and motion perception. Di Dona et al.'s (*in preparation*) work and the present one could aid in the implementation of a new perspective - the one of brain oscillations - to the understanding of RM and motion perception in general.

As mentioned above, Senior et al. (2002) used TMS to stimulate +hMT/V5 and observed the cancellation of RM effect in a static image paradigm. As opposed to this, Rao et al. (2004) used fMRI and found no increased activity of +hMT/V5 in an apparent motion task. To explain this, they suggested an involvement of a fronto-parietal network. On the other hand, we utilized continuous rotational motion (see 2.2). It could be argued that a fronto-parietal network is related to the perception of discrete or static stimuli, therefore using tACS to impose a frequency within the beta band could have a greater effect on a RM task using discrete motion stimuli. In addition to this, a broader stimulation layout, targeting PFC as well as PPC, could clarify the role of a fronto-parietal network in explaining RM and displacement.

As Engel and Fries (2010) noted, BBA is increased if a strong top-down endogenous control is needed in a cognitive task (see 1.3.1). Therefore, it is possible that utilizing a different paradigm which involves more symbolic stimuli and decisions over the task (for a review, see Hubbard, 2005; 2014) could lead to a greater BBA and therefore to a stronger effect of beta-tACS on the task.

4.2 Limits and future developments

The already mentioned very small sample size is a strong limit, because it significantly increases the noise within the data, thus lowering statistical power. Indeed, very weak conclusion have been drawn from the collected data. Furthermore, the high number of sessions and the length of the single sessions could have led to fatigue in the participants, possibly contributing to the high variability observed in the data. However, the number of sessions is difficult if not impossible to decrease, this is because of the necessity of a sham stimulation condition as control, in order to assess that the measured effects are caused by electrical stimulation; and of a different frequency stimulation condition (theta) compared to the experimental stimulation condition (beta) as another control, in order to assess frequency-specific effects on the task.

Future studies should explore the relationship between beta oscillations and motion perception more deeply, perhaps utilizing different kinds of motion perception tasks in order to understand whether beta oscillations are more related to a general mechanism of motion perception in the dorsal stream or they correlate more strongly with motion prediction and extrapolation. Furthermore, future works could also monitor eye movements, as it is known that they could be a confounding variable if not controlled (Kerzel, 2000, 2006).

Chapter 5 – Conclusion

The present work was designed to contribute to the understanding of the relationship between beta oscillations and motion perception, utilizing transcranial alternating current stimulation (tACS). The dorsal stream and PPC play a crucial role in motion perception, which is why we decided to target these areas with electrical stimulation. A largely studied phenomenon in motion perception is Representational Momentum, which describes how the brain predicts the future location of a moving object: if such object disappears in its trajectory, the perceived vanishing location is displaced forward in the direction of motion.

Following a recently discovered correlation between BBA and the forward tilt of a rotating bar (Di Dona et al., *in* preparation), we subjected participants to the same task, and we administered three kinds of stimulations (within beta and theta frequencies and sham) on the parietal cortex in order to assess a specific contribution of beta frequency in motion perception. We expected to see a cancellation of the RM effect when administering beta-tACS. However, the results do not support the original hypothesis.

There was no stimulation-induced modulation of the RM effect and only a numerical tendency of beta-tACS in reducing the effect of speed. In addition, we observed that beta-tACS reduced the general accuracy in the task. These results are not highly reliable because of the high level of noise and variability, which is a consequence of the strongly reduced sample size. However, it can still be argued that beta oscillations play a role in motion perception that could pertain to other mechanisms rather than motion extrapolation and prediction.

The study featured in this work, even considering the low statistical power, nevertheless contributes to the understanding of the role of neural oscillations in the perception of movement. It is, to our knowledge, the first causal study on RM and neural oscillations and thus provides the ground for future studies on this topic.

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Supplementary Materials

Exclusion criteria questionnaire for tES/TMS (Antal et al., 2017).

Before undergoing Transcranial Magnetic Stimulation (TMS) or Transcranial Electrical Stimulation (tES) please read and answer the following questions. The information you provide is strictly confidential and is used to minimize risk factors when using these techniques.

Do you suffer or have you ever suffered from seizures, febrile convulsions, or recurrent faintings?	**YES**	**NO**
Do you have a family history of epilepsy? If YES please indicate the degree of relatedness of the family member(s)	**YES**	**NO**
Have you ever suffered a traumatic brain injury? If Yes please provide details below.	**YES**	**NO**
Do you have metal inserts in your skull (surgical clips "in your head")?	**YES**	**NO**
Do you have any heart conditions?	**YES**	**NO**
Do you have a pacemaker in your heart?	**YES**	**NO**
Do you take tricyclic antidepressants?	**YES**	**NO**
Do you take neuroleptic medications?	**YES**	**NO**
Do you suffer from severe and frequent headaches?	**YES**	**NO**
Have you had more than three units of alcohol in the past 24 hours?	**YES**	**NO**
Have you had more than 2 cups of coffee or caffeine from other sources in the last 2 hours?	**YES**	**NO**
Have you used any drugs in the last 24 hours? If YES please indicate which	**YES**	**NO**
Have you participated in other experiments with tRNS before?	**YES**	**NO**
Are you right-handed or left-handed?	**R**	**L**
<u>Women only:</u>		
Are you in a definite or presumed state of pregnancy?	**YES**	**NO**

Date of birth ________________ Padova, ______________

Signature_____________________