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BRAIN SIGNALS OF PERCEPTUAL INFERENCE: THE ROLE OF OSCILLATIONS IN INTERPRETING AMBIGUOUS STIMULI

Dissertation to obtain a Master’s degree in Biomedical Engineering,
supervised by Gabriel Nascimento Ferreira da Costa (PhD) and presented to the Physics Department
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FACULDADE DE CIÊNCIAS E TECNOLOGIA
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Sinais cerebrais de inferência percetiva: o papel das oscilações na interpretação de estímulos ambíguos

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“Imagination is more important than knowledge. Knowledge is limited.
Imagination encircles the world.”
Albert Einstein

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Abstract

When sensory information is ambiguous and consistent with two exclusive interpretations in the absence of information that could make perception converge to only one interpretation, spontaneous perceptual reversals occur every few seconds between the two possible interpretations. This phenomenon is called bistable perception. The role of the beta band activity (13-30 Hz) in cognitive processes is still unclear, especially compared to other frequency bands. Moreover, despite evidence that beta activity is related to bistable perception and suggesting a role for beta activity in disambiguating perception, its actual function is yet unknown. Whether the activity of this band signals the maintenance of the *status quo* or the presence of the dominant percept, there is an enormous controversy around the part the beta-band activity plays during bistable stimulus.

The present work explores the behaviour of beta-band oscillations during ambiguous perception. The main hypothesis of the current work is that beta activity is increased when the brain perceives a dominant percept and decreases when an alternative configuration is perceived. In order to study this relation between beta activity and perceptual dominance or bias, a psychophysical study with healthy volunteers perceiving a bistable stimulus was performed. In this way, the first part of the experiment focuses on the study of two ambiguous stimuli: a visual one, Stroboscopic Alternative Motion (SAM) entailing ambiguous motion; and an auditory one of auditory streaming, which also results in bistable perception. This part focused on determining how to bias the perception of the subject towards one percept, by changing the value of one characteristic of the stimulus. The second part focuses in recording the brain oscillations while the subjects perform these same bistable paradigms. For that it was chosen the Electroencephalogram, since this technique has an adequate spatial coverage of the brain activity and high time resolution, in addition to being non-invasive and low cost. After the acquisitions, frequency analysis and time frequency analysis were performed to study the differences in beta oscillations in moments where the perception was stable and moments where a reversal occurs.

The results show that a successful control of each subjects' perceptual bias was achieved, that is, regardless of interindividual difference in the relative dominance of distinct percepts, individual calibration provided optimal parameters to bias perception towards specific percepts for all subjects. Using experimental conditions that veered perception towards one percept or the other, it was found that, nonetheless, perceptual dominance does not entail significant changes in the activity of beta band during perceptual reversals. To be sure, there is in fact a decrease in beta oscillations before the change and an increase after the change, but the amplitude of beta oscillations is similar between both perceptual configurations. This was observed for both visual bistability and auditory, suggesting there is no correlation between the probability of perceiving a particular percept, i.e. between a percepts dominance, and beta activity. It remains an open question whether beta oscillations, despite having been found to be not responsible for biasing perception, still have a role in the brain alternating between percepts and in settling for - or perhaps in maintaining - either of two valid percepts.

Keywords Vision, Brain Oscillations, Perception, Ambiguity, EEG.

Resumo

Quando a informação sensorial é ambígua e consistente com duas interpretações exclusivas sem qualquer informação que possa fazer a perceção convergir para apenas uma interpretação, trocas percetuais espontâneas ocorrem em poucos segundos entre as duas possíveis interpretações. A este fenómeno chama-se perceção biestável. O pepel da atividade da banda beta (13-30 Hz) em processos cognitivos ainda não é claro, especialmente se comparado ao de outras bandas de frequência. Além disso, apesar de existirem evidências que a atividade beta está relacionada com perceções biestáveis e que sugerem um papel da atividade desta banda na desambiguação da perceção, a sua função atual é ainda desconhecida. Quer a atividade beta sinalize a manutenção do *status quo*, quer a presença da perceção dominante, há uma enorme controvérsia acerca do papel que a atividade da banda beta tem em estímulos biestáveis.

O presente trabalho explora o comportamento de oscilações da banda beta durante perceções ambíguas. A principal hipótese deste trabalho é que a atividade beta aumenta quando o cérebro percebe uma perceção dominante e diminui quando a configuração alternativa é percebida. De forma a estudar esta relação entre a atividade beta e a dominância percetual, foi feito um estudo psicofísico com voluntários saudáveis que respondiam a estímulos biestáveis. Desta forma, a primeira parte do trabalho incide no estudo de dois estímulos ambíguos: um visual, Movimento Alternativo Estroboscópico (SAM) implicando movimento ambíguo; e um auditivo de *streaming* auditivo, que também resulta em perceção biestável. Esta parte foca-se em determinar um método para influenciar a perceção do sujeito para uma interpretação, mudando o valor de uma característica do estímulo. A segunda parte deste estudo incide na aquisição de oscilações cerebrais enquanto os participantes realizam os mesmos paradigmas biestáveis. Desta forma, foi escolhido o Eletroencefalograma, devido a esta técnica ter uma cobertura espacial adequada da atividade cerebral e alta resolução temporal, além de ser não invasiva e de baixo custo. Após as aquisições, análises de frequência e análises de frequência temporal foram realizadas de forma a estuar as diferenças em oscilações betas em momentos de perceção estável e momentos de ocorrência de uma reversão da interpretação.

Os resultados mostram que foi alcançado um controlo bem-sucedido do viés percetual, isto é, independentemente da diferença inter-sujeitos da dominância relativa de perceções distintas, a calibração individual forneceu parâmetros ótimos para enviesar a perceção para uma interpretação especifica para todos os voluntários. Usando condições experimentais que desviam a perceção para uma interpretação ou para a outra, foi descoberto que, não obstante, a dominância perceptual não implica alterações significativas na atividade da banda beta durante trocas percetuais. Contudo, existe, de facto, um decrescimento nas oscilações beta antes da troca percetual e um crescimento da sua atividade depois da troca, mas a amplitude destas é semelhante em ambas as configurações percetuais. Esta situação foi observada para ambas as situações de biestabilidade, visual e auditiva, sugerindo não existe correlação entre a probabilidade de perceber uma perceção particular, i.e. entre a dominância de perceções, e a atividade beta. Assim, esta questão continua aberta, se as oscilações beta, apesar de se ter descoberto que não são responsáveis por enviesar a perceção, sempre têm um papel na alternância entre percepções e em decidir (ou talvez em manter) entre duas perceções válidas.

Palavras-chave: Visão, Oscilações cerebrais, Perceção, Ambiguidade, EEG.

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1. INTRODUCTION

In the introductory section of the work some concepts are explained in order to justify the motivation of the present work. It starts with a review of neuroanatomic concepts about the visual and auditory cortices, to better comprehend where are located the brain centres that process sensory information. This is followed by a brief synthesis of the brain oscillations. As the goal of this work is to study the behaviour of beta oscillations in situations of ambiguity, this topic will be introduced to better understand what ambiguity is. In the end, there is an explanation of the technique used to assess the goal of the work, the Electroencephalogram (EEG).

1.1. Motivation

There are much to know, yet, about the mechanisms behind perception. How the conflict with ambiguous stimulus is resolved and which parts of the brain take part in this process are still unsolved questions. There is a large body of evidence of an involvement of beta band activity in perception under ambiguity with some authors suggesting a role in mechanisms of perceptual decision, while other theories postulate that the activity of this band is related to maintenance of perceptual stability, a cognitive *status quo*. In this study, it is intended to clarify the role of these oscillations in bistability, because a systematic study on this topic is missing and would be of great importance in unifying several findings that have until now seem disparate in the study of beta oscillations role. With this goal, it was used an ambiguous visual stimulus and an ambiguous auditory stimulus. The choice of the first stimulus comes from the existence of vast studies about this kind of stimuli which give a degree of certainty about the best procedures to follow in this work. On the contrary, the decision to use an auditory stimulus, as well, is due to fact that there is a lack of studies using it and it offers an opportunity to assess if there is any relation between these two types of bistability.

1.2. Visual Cortex

The visual cortex is the area of the brain responsible for receiving, segmenting, integrating and processing the visual information. This area of the brain extends from the occipital lobe to temporal and parietal lobes and is divided in two main areas according to its function and structure: V1 also known as striate or primary visual cortex; and extrastriate cortex composed of V2, V3, V4 and V5 areas.

The image processing starts at the retina where light is converted in chemical signals transmitted to the thalamus through the optical nerve and then relayed to the visual cortex. When visual information arrives at the visual cortex, it finds the striate cortex, or V1, where simple cells with a small receptive field respond to elementary visual information, like lines of a specific orientation. After V1 has received visual information, it sends it to V2 and V3, where information is differentiated between object orientation and colours, for example, by more complex cells that are found in regions further in the visual processing pathway. These cells can be built by combining inputs from multiple sources, including multiple simple cells from more primary cortical areas, resulting in cells that can be sensitive to features such as motion, colours and shapes. After this, information is sent to other areas and is divided into ventral and dorsal streams. The dorsal stream is specialized in processing spatial tasks and visual-motor skills and the ventral stream processes recognition of objects. The visual processing is almost totally unconscious, this fact can make some misinterpretations happen, that can be seen by the efficiency of visual illusions. Throughout the visual pathway, from retina to the visual cortex, a spatial organization referred to as retinotopy is maintained (Figure 1.1). This retinotopic organization arises from a spatial relation between adjacent retinal areas that sample contiguous areas of the visual field, which is preserved up until the initial processing of vision in the extrastriate cortex. (Purves, 2004; Huff,, 2019)

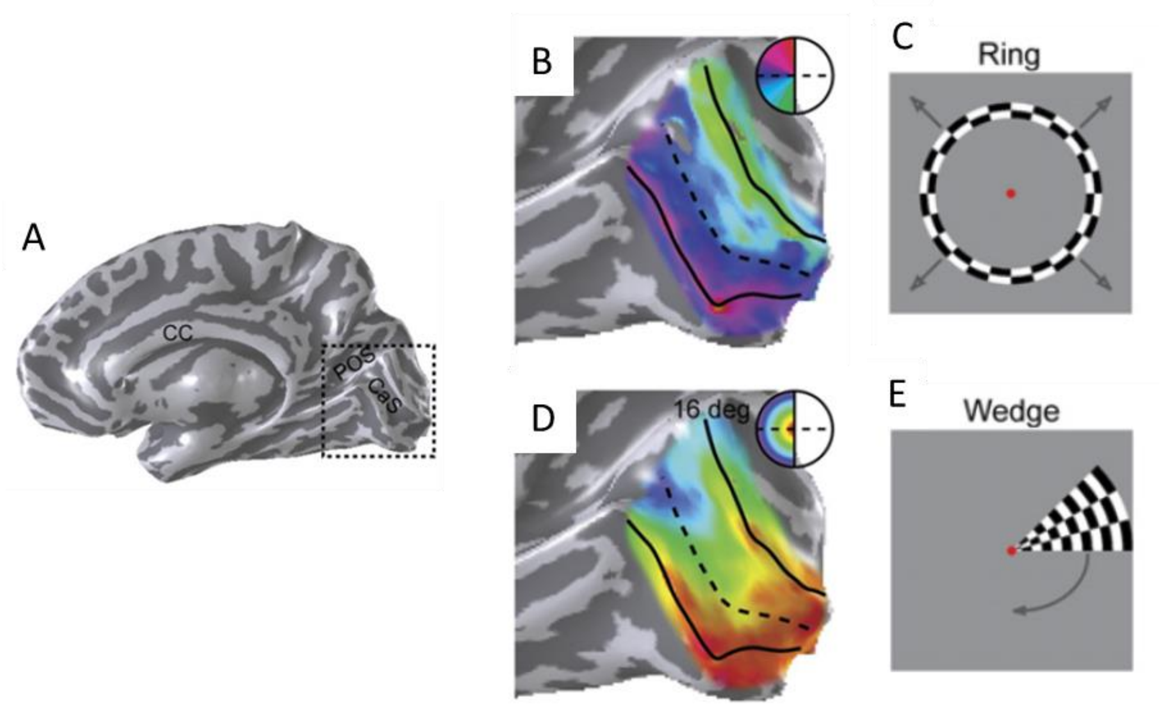

Figure 1.1. Visuotopic organization of the human visual cortex. A) Section of the righ hemisphere of the human brain; CC is corpus calosum, POS is the parietal-occipital sulcus and CaS is the calcarine sulcus. B) Highlighted area represents the retinotopic map of eccentricity of the early visual cortex, mapped using expanding rind (C). D) Highlighted area represents the retinotopic map of visual angle the early visual cortex, mapped using rotating wedge (E). (Adapted from Wandell et al., 2007).

1.3. Auditory Cortex

The auditory cortex is the last stop of the auditory information path. The auditory cortex is divided in two areas, the primary and the peripheral, also called, belt. The former is located in the temporal lobe, more specifically in the superior temporal gyrus. The ventral division of the medial geniculate complex gives point-to-point input to the primary area of the auditory cortex. This area has a tonotopic map, which is the spatial arrangement of where sounds of different frequencies are represented in a continuum. Hence, like in the visuotopy of the visual cortex, similar sounds in terms of frequency are neighbours in this map. On the other hand, the belt areas are receptors of more diffuse input and thus have a less precise tonotopic organization. The primary auditory cortex has a topographical map of their correspondent sensory epithelia, in this case of the cochlea. The cochlea is the most important structure in the auditory pathway, it is in there that the energy from generated pressure waves is converted into neural impulses. The cochlea decomposes the acoustical stimulus, so it is here that the tonotopic arrangement is first established, along the length of the basilar membrane. Binaural properties are arranged in stripes that are orthogonal to the frequency axis of the map. This arrangement is a combination of alternative stripes of neurons, ones that are excited by both ears (EE cells) and others that are excited by one ear and inhibited by the other (EI cells). According to whether the stimulation is ipsi- or contralateral, the auditory cortex gives a different response. Other higher order areas of the auditory system responsible for the comprehension of speech, the Wernicke’s area, is posterior to and apart from the auditory cortex (Purves, 2004).

Figure 1.2. represents the auditory cortex in the brain and its tonotopic organization.

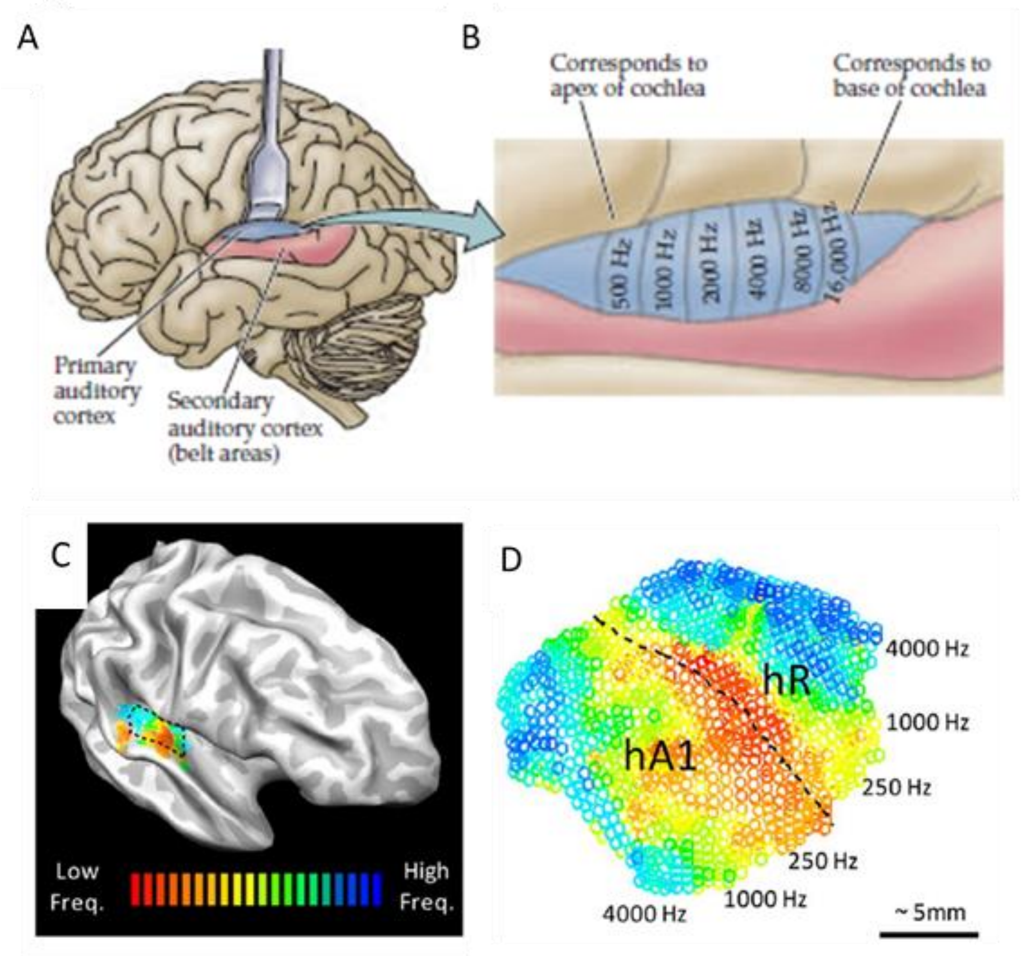

Figure 1.2. Representation of the tonotopic organization of the human auditory cortex. A) Diagram of the brain in left lateral view showing the primary cortex. B) Tonotopic organization of the primary auditory cortex (Adapted from Neuroscience). C) Mapping of the human auditory cortex, representated in inflated right lateral view. D) Voxelization of the highlighted region in C, each voxel represents the frequency to which that area is tuned, from 80Hz to 8000Hz. (Adapted from Purves, 2004, Saenz and Langers, 2014).

1.4. Brain Oscillations

Brain oscillations were first recorded in humans by Hans Berger (1873-1941), the inventor of Electroencephalography (Basar, 2013). These oscillations are repetitive and rhythmic electrical activity that is generated spontaneously and can be modulated in response to changes in mental activity and with stimuli reaching the central nervous system (Basar, 2013). Brain oscillations display a striking consistency over different mammalian orders (Figure 1.3) and have been found to play a role in controlling the timing of neuronal firing (Varela et al., 2001). For instance in the hippocampus there is a strong dependency of the firing of neurons on the phase of ongoing oscillations (Bastos et al., 2015), namely theta (see below), which also provides a dynamic scaffold for sequentially activated neurons (Buzsáki, 2006). Moreover, recently it has been proposed that oscillations, particularly gamma, can serve a role of temporally coordinating the transfer of information between brain regions (Varela et al., 2001, Bastos et al., 2015).

There are five classical frequency bands that brain oscillations are divided in (Buzsáki, 2006):

- Delta: 0.5 – 4Hz;
- Theta: 4 – 8Hz;
- Alpha: 8 – 12Hz;
- Beta: 12 – 30Hz;
- Gamma: >30Hz.

Most of these oscillations can be found over several brain areas in the awake human EEG. For instance, alpha, beta and gamma are fairly prominent in the central areas during motor execution and somatosensory stimulation (Cheyne, 2013), gamma is prevalent in subcortical areas such as the hippocampus, and theta oscillations are found in both high order cortical areas such as the prefrontal cortex as well as in the hippocampus (Buzsáki, 2006).

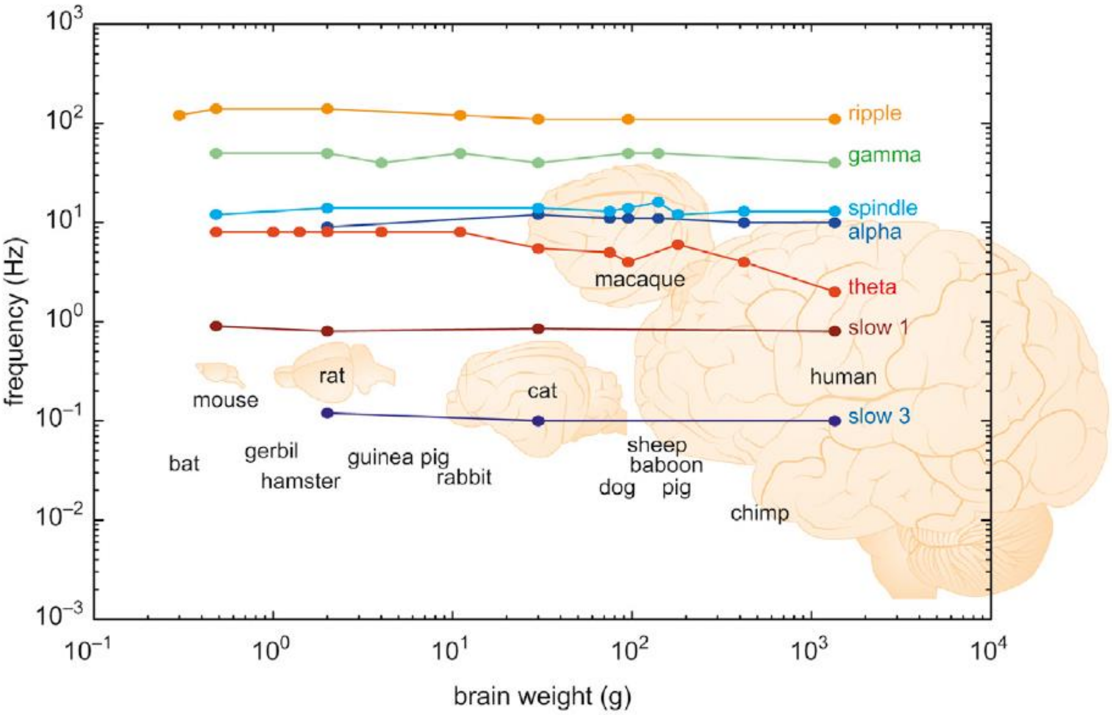

Figure 1.3. Brain rhythms are conserved across different species. Diagram of the brain of different species, indicating the respective median weight and the oscillations present in their brains. (Adapted from Buzsaki et al., 2013).

Oscillations of different frequency bands are related to different states of the brain and serve different functions (Steriade et al., 1993, Knyazev, 2007). Oscillations from delta-band are the predominant during deep sleep and are linked with learning, brain reward system and motivational processes (Fries, 2009). The theta-band corresponds to activity associated with working memory functions, fear conditioning and emotional arousal (Jensen and Lisman, 2005). Activity in the alpha-band reflects cortical activity during the awake resting-state, usually associated with an idling state of the cortex when sensory input is reduced (Palva and Palva, 2007). Nonetheless, alpha oscillations have recently been revealed to entail a much more active role of disengaging task-irrelevant brain areas by actively gating sensorial input, as well as playing a crucial role in working memory function and short-term-memory retention (Palva and Palva, 2007). The gamma-band is the focus of many studies regarding cognition and consciousness and many cognitive roles have been attributed to this, including feature integration, stimulus selection, sensorimotor integration, movement preparation, attention, memory formation and awareness (Engel and Fries, 2010). Beta-band oscillations have been mainly studied for its sensorimotor functions (Cheyne, 2013), but its role in cognitive functions remains unclear.

1.5. Perception

Perception is the organization, identification and interpretation of sensory information in order to form a mental representation (Schacter et al., 2011). The mechanisms that give rise to perception reside in the central nervous system, where sensorial signals arrive after the sensory organs are stimulated (Goldstein, 2010). Beyond these signals, perception is dependent on the observer's own internal state and experience, which then relates to learning, attention, expectation and memory (Gregory, 1973, Bernstein, 2011). Perception is a process that can take place without requiring attention and awareness, but that still depends on complex functions from the nervous system (Goldstein, 2010). The study of perception revolves around two major areas in Neuroscience: Psychophysics and Sensory Neuroscience. The first studies the relationship between physical qualities of the sensory input and their perceptual properties. The second studies the mechanisms behind perception as they relate to neuronal signals and the activity of sensory organs (Gregory, 1973).

Illusions and multistable perceptions have shown that the perceptual systems of the brain can be viewed as being an active and conscious attempt to decode their input, instead of a passive organ with only input-driven activity (Gregory, 1973).

In this sub-section, the concept of multistability is clarified and how it works in the visual and auditory fields.

1.5.1. Multistable Perception

Multistable perception is a phenomenon that manifests when sensory information is consistent with two or more competing interpretations. In these situations, there is no information that makes a subject perception converge to only one interpretation (Sterzer et al., 2009). This causes a spontaneously alternation every few seconds between two or more interpretations of the same sensory input, leading to bistability in the first case and multistability in the second. Despite being spontaneous and unavoidable, perceptual reversals are partialy influenced by cognitive mechanisms and volitional control (Eagleman, 2001).

Multistable phenomena have some supramodal mechanisms in common, such as regions of the brain involved in the resolution of multistable conflict (Sterzer and

Kleinschmidt, 2007) and physiological effects, like pupil dilatation around perceptual transitions (Einhauser et al., 2008). Different subjects have different performances under multistable perception tasks, and this can be explained by factors such as genetic predispositions (Chen et al., 2018) and neurotransmitter balance (Kondo et al., 2017).

The study of multistable perception still remains very fertile particularly with the appearance and improvement of non-invasive brain imaging techniques. A crucial advantage of this class of stimuli is that it allows one to distinguish the neural activity resulting from physical stimulus properties from that arising from the conscious perception of it. This is the reason why multistable perception is a great tool to comprehend the neural processes that generate a coherent subjective experience of the world, which often relies on information that is fragmentary, conflicting and even ambiguous (Sterzer et al., 2009).

During tasks involving multistable stimuli there are two main internal mental states: states of transition between perceptual configurations, also known as percepts, and states of maintenance of a competing configuration (Rees, 2001). The first, refers to when the perception, usually involuntarily but also under volitional control, switches and is relatively quick, hence two configurations do not coexist for longer than a brief period or not at all (Rees, 2001). The second refers to the states when perception is constant, hence a single configuration is perceived stably, and lasts longer than reversals (Rees, 2001). Recently, a study by Sen et al (2020) attempted to classify these two mental states of the brain on a single-trial basis using several paradigms of visual bistability. This work successfully classified these states with high accuracy above chance level and it was also observed that sources from the occipital lobe, parietal lobe and cerebellum were involved in discriminating these states.

1.5.2. Visual Multistability

While multistability can occur through virtually all senses, most studied paradigms involve visual multistability (Eagleman, 2001). There are many visual multistable phenomena, like Necker’s cube, binocular rivalry (BR), pattern-component rivalry, structure from motion, motion induced blindness, figure-ground, Lissajous figure and stroboscopic alternative motion (Brascamp et al., 2018). Figure 1.4 represent some of the multistable visual stimuli most frequently used in the literature.

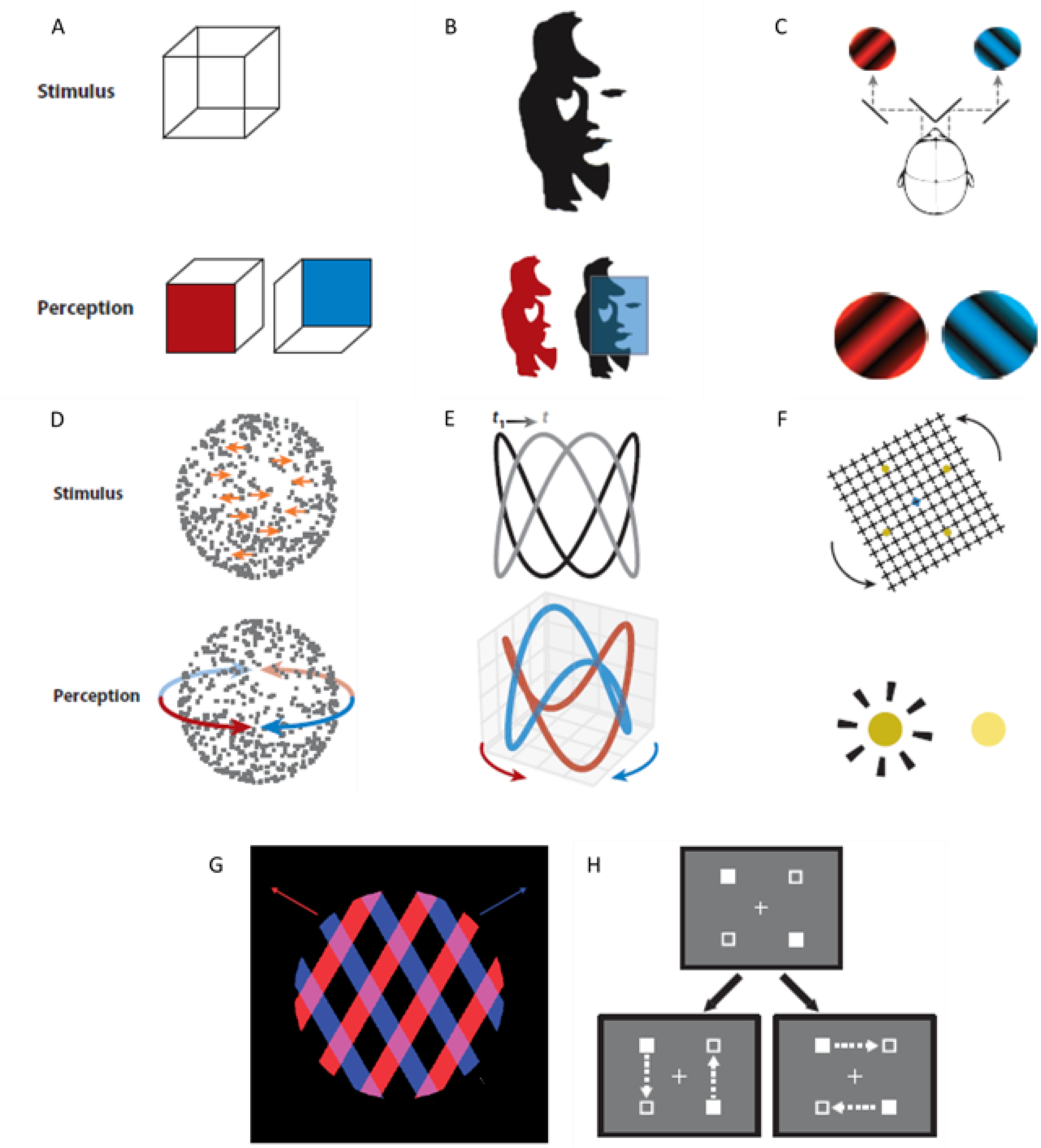

Figure 1.4. Forms of visual multistable phenomena. All stimuli above are depicted with original stimulus on top and the competing percepts that result from it below. A) Necker's cube, with two possible interpretations: pointing up or pointing down. B) Figure-ground. Several examples exist of this kind of image. The Rubin vase also belong to this category. C) Binocular rivalry (BR). In BR only one image emerges from the presentation of conflicting stimuli to distinct eyes. D) Structure from motion. 3D motion can often be ambiguous and thus rotation can be interpreted in either a clockwise or counter clockwise direction. E) Lissajous figure. Similar to structure from motion. F) Motion induced blindness. Dots visible in the background briefly disappear due to the moving pattern (for an interactive demo see https://michaelbach.de/ot/mot-mib/index.html). G) Plaids or Pattern-component rivalry. Stripes can be seen as moving in a single direction or sliding past each other. H) Stroboscopic alternative motion (for an interactive demo see https://michaelbach.de/ot/mot-sam/index.html) . Adapted from (Genc et al., 2011, Brascamp et al., 2018, Einhauser et al., 2019)

A study by Cao et al (2018) made their participants perform 11 tasks, each with a different visual multistable stimulus for 3 min and concluded that different phenomena share some underlying mechanisms. Nonetheless, identifying brain regions involved in resolving the conflict of ambiguous stimuli is still a challenging task and much remains up to speculation.

The centres of the brain that reorganize activity through the visual cortex during perceptual reversals have been found to be non-sensorial, with frontal and parietal cortex having a causal role in perceptual reversals during multistability (Leopold and Logothetis, 1999). Electrophysiological recordings in monkeys have shown percept-specific activity during bistable motion perception in parietal cortex (Williams et al., 2003) and motion-sensitive areas V5/MT (Dodd et al., 2001). In humans also perceptual reversals in bistable visual stimulus with an ambiguous motion direction are associated with distinct responses by motion responsive areas, like V5/MT (Castelo-Branco et al., 2002). The distinct activity during perceptual reversals could reflect the reorganization of neuronal activity within the visual cortex (Leopold and Logothetis, 1999), or they might only relate to the feed-forward communication of neural events from visual cortex to other areas (Attneave, 1971, Blake, 1989). Raemaekers et al (2009) propose that there is an involvement of frontal and parietal regions in the regulation of stability during bistable motion perception. Stezer and Kleinschmidt (2007) have shown a greater BOLD contrast fMRI signal in bilateral inferior prefrontal cortex in spontaneous perceptual reversals in bistable motion perception, suggesting this area might contribute to perceptual dynamics.

Multistable perception can thus be considered the product between interactions of ‘low-level’ (sensory) and ‘high-level’ (frontal and parietal) brain regions (Sterzer et al., 2009). It was found increased activity in the parietal cortex in reversals during a presentation of the Necker cube (Britz et al., 2009). This activity might also contribute to the stabilization of a percept, an effect that can be observed under certain intermittent presentations of the ambiguous stimulus (Leopold et al., 2002).

If an ambiguous visual stimulus is presented intermittently, the observer tends to start perceiving the percept they were perceiving when the stimulus was interrupted, suggesting some form of short-term memory might play a role in perceptual decision (Pearson and Brascamp, 2008). However, in the absence of such memory effects, the activity in extrastriate visual cortex can bias perceptual choice (Leopold and Logothetis, 1999). This means that when an ambiguous stimulus is presented during long periods, the percepts have a stochastic behaviour (Hesselmann et al., 2008). This suggests that multistability involves a constant re-evaluation of the current interpretation of the sensory input (Leopold and Logothetis, 1999).Nonetheless, it is still a mistery how the brain decides which percept should be interpreted (Sterzer et al., 2009).

All multistable phenomena have the following properties: exclusivity, ambiguous visual interpretations are never simultaneously present; inevitability, the process of perceptual alternation is a passive and automatic process; and randomness, the duration of each percept and the moment they switch is random and the duration of one percept does not influence the duration of the next one. These aspects show that reversals do not come only from a single mechanism of satiation, but probably from influence of central and sensorymotor areas in the visual system (Leopold and Logothetis, 1999). This stochastic effect can become more deterministic with voluntary control or with a change of the sensory input but despite this perceptual reversals are mostly involuntary actions (Leopold and Logothetis, 1999).

Perceptual transitions are related to the expression of a behaviour which means, they occur spontaneously and are influenced by attention and mood, both subjective variables. These reversals become easier with practice and can be compromised if lesions happen in non-visual cortical areas. Reversals have temporal dynamics like those in behaviours that are initiated spontaneously. The average time that an observer spends perceiving a percept during multistable perceptions is influenced by holistic properties, like symmetry, closure and element proximity (Koffka, 1935) and by high-level properties, like recognizability and semantic content (Walker, 1978).

A study by Lack (1978) found that the reversal rate increased 3 to 8 times after 10 days of practice and other studies have a large body of evidence that perceptual reversals need to be learned to achieve perceptual multistability (Rock and Mitchener, 1992). Various factors can influence perceptual alternation, like intelligence, personality variables and even mood disorders (Crain, 1961, Meredith, 1967). Some agents like caffeine and sodium amytal can influence this rate in BR and reversible figures (George, 1936). Ricci and Blundo (1990) found that patients with frontal lobe damage had the ability to switch from one subjective view to the other of an ambiguous figure impaired, but patients with lesions in posterior cortical areas had no difficulties in perceiving reversals comparing to control subjects.

Difficulty in shifting perspective is restricted to patients with lesions in right frontal brain areas (Meenan and Miller, 1994).

1.5.3. Auditory Multistability

Auditory illusions have provided optimal stimuli to help understand how the brain forms auditory percepts (Kondo and Kashino, 2007).

Two phenomena of auditory multistability have been extensively studied:

- **Verbal Transformations**

Verbal Transformations consist of listening to a word repeated continuously, which results in a series of illusory transitions that are perceived as the word is physically changing, when in fact it is not (Kondo and Kashino, 2007). For example, the repetition of the word “tress” can make the subject to perceive the word as “dress”, “stress”, “drest” and “Esther” (Warren and Gregory, 1958, Warren, 1961). Two processes influence this stimulus: satiation and criterion (Warren and Warren, 1966, Warren, 1985). If the stimuli are repeated, the stored information is satiated which causes a change in the criterion that discern the boundaries of the speech sounds and leads to perceptual transitions in the perceived word (Kondo and Kashino, 2007).

It was found that with this stimulus, the verbal forms depend on how a word phonetically reorganizes, rather with lexical distortion and auditory adaptation (Kondo and Kashino, 2007). Also, brain activity causing individual differences in perceptual transitions and tone detection has been identified (Kondo and Kashino, 2007). With this, it is possible to think that distributed frontal areas - the left supramarginal gyrus (SMG), left inferior frontal cortex (IFC), and anterior cingulate cortex (ACC) - can be involved in the processes that contribute to verbal transformations, and not in processes of auditory-specific areas (Sato et al., 2004).

- **Auditory Streaming**

Auditory Streaming is a bistable auditory stimulus in which a sequence of tones is presented to the observer that can be perceived either as one stream or more than one stream of sound (Pressnitzer and Hupe, 2006). Spontaneous alternations are inevitable between percepts of one or two streams (Pressnitzer and Hupe, 2006) when the stimulus is presented for a prolonged time (Noorden, 1975). A study by Billig *et al* (2018) using auditory streaming with subjects being asked to maintain one percept at a time concluded that it was possible for the listeners to partially influence how many streams they were perceiving.

The dominancy of one percept over the other is dependent on how far apart the frequency of the two tones are (Kondo and Kashino, 2009). Kondo and Kashino (2009) studied this stimulus with different semitone differences between tones and combine with fMRI to assess how the temporal dynamics of the activity of the brain differs according to the direction of perceptual reversals. Activity in the auditory cortex was recorded in perceptual transitions from dominant to non-dominant percept. Perceptual reversals from non-dominant to dominant percept showed a greater activity in the medial geniculate body (MGB) and in this way, the activity in these brain regions depends on the dominant percept (Kondo and Kashino, 2009).

1.6. Electroencephalogram

Electroencephalogram (EEG) is the recording of the electrical activity of the brain from electrodes placed in the scalp (Rangayyan, 2005). The signal of EEG is the sum of the electrical activities of population of neurons, which are excitable cells that generate electrical and magnetic fields (Niedermeyer and Lopes da Silva, 2005). In this way, cortical potentials are produced due to inhibitory and excitatory postsynaptic potentials that are developed by pyramidal neurons,(Niedermeyer and Lopes da Silva, 2005, Rangayyan, 2005). This means, their activity can be recorded by surface electrodes placed at the small distances or even at the scalp if the activity involves a sufficiently large number of cells (Niedermeyer and Lopes da Silva, 2005, Rangayyan, 2005).

EEG is a high-temporal technique with some advantages that justify its common use in neurophysiology and psychology. The first advantage is the fact that this technique acquires the dynamic of cognitive processes in the time frame in which it occurs. These processes are very fast, occurring within tens to hundreds of milliseconds, and this technique has a high temporal resolution which is very suitable to study these events. The second advantage is the fact that EEG measures directly the neural activity. The EEG measures voltage fluctuations that represent the biophysical phenomena occurring at the level of populations of neurons and oscillations observed in the EEG signal reflects the neural oscillations from the cortex. The third advantage of EEG technique is comprising four dimensions. They are time, space, frequency, and power and phase (power and phase are both discrete elements of one dimension). The fact that EEG is multidimensional gives a lot of possibilities to specify or test hypotheses in the fields of neurophysiology and psychology. (Cohen, 2014)

2. BACKGROUND AND GOAL OF THE PROJECT

This section aims to explain the background that motivated this work and the state of the art about the concepts this work has studied. In the end, the goals of the work are presented.

2.1. Beta oscillations in cognition

The role of beta band oscillations was first identified in its relation with motor responses and the most part of the literature explores this function, both in health and in diseases, such as Parkinson (Engel and Fries, 2010). Nonetheless, over the past decade a more cognitive function of beta has been acknowledged.

Beta-band activity is diminished in voluntary movement but is pronounced during steady contractions and in rest periods after a movement (Baker, 2007). However, when a subject is preparing or executing a movement, beta activity undergoes a reduction in amplitude while gamma oscillations increase (Schoffelen et al., 2005, Donner et al., 2009). This may indicate, the activity from beta-band oscillations may promote the maintenance of the actual motor set while limiting or blocking the neural processing of new movements (Pogosyan et al., 2009). A study by Pogosyan et al (2009) manipulated the behaviour of subjects by inducing a 20Hz rhythm into the motor cortex, whilst subjects were performing a visuomotor tracking task. It was possible to find that the voluntary movement velocity of the subjects was decreased. Baker et al (2007) suggested that oscillations in the beta-band are due to the monitorization of the *status quo* and the recalibration of the sensorimotor system. There are reports of beta-band activity being modulated according to what is expected of a forthcoming event (Engel and Fries, 2010) and a study by Donner et al (2009) showed there are changes in beta band activity in motor and premotor cortex some seconds before a decision is executed, which means this changes occur when a decision is being made. If a subject thinks that the probability of executing a motor response decreases, the activity of beta-band oscillations increases cortico-spinal coherence (Schoffelen et al., 2005). These show that beta band activity is related to mechanisms with the goal to maintain the *status quo* and there is evidences that characteristic might not be just for motor control domain, but for cognitive processes, as well (Engel and Fries, 2010).

Regarding the role of beta-band oscillations in cognitive processes, it has been proposed that the activity of these oscillations is high during tasks involving top-down signaling and their activity shows a decrease with bottom-up activity, existing in this case an increase in the gamma-band activity (Fries, 2009, Engel and Fries, 2010). Top-down components come from more complex and specialized brain areas, instead of bottom-up components, that come from early sensory areas of the brain through feed-forward signalling. For example, in the visual stimulus of Stroboscopic Alternative Motion, seeing the circles involves bottom-up factors, but perceiving a motion instead of the other likely involves top-down signaling. During auditory ambiguous stimulation the perceptual reversals appear correlated with beta-band activity, suggesting a triggering of reversals by beta activity (Iversen et al., 2009). Studies made by Buschman and Miller (2007, 2009) in monkeys suggested that top-down attention has a communication through beta-band oscillations, but when information needs to be transferred as bottom-up signals, those oscillations change to faster ones, that is, gamma-band oscillations. Engel and Fries (2010) propose that beta-band activity is increased when the the current state, i.e the default state or *status quo*, is prioritized over new signals, contrary to gamma-band activity which is increased when there is a change in stimulus and brain states.

2.2. Visual Multistability *vs* Auditory Multistability

A study by Pressnitzer and Hupe (2006) compared auditory streaming with bistability associated with visualizing plaids in order to assess whether auditory streaming is a true bistable percept. Prior studies (see Anstis et al., 1985) did not consider auditory streaming as bistable since segregated was the dominant percept throughout most of the task, perhaps owing to a short stimulus duration. Pressnitzer and Hupe (2006) used longer periods reaching the 240s that lead to the opposite conclusion. After the first percept, there was no long-term trend and the steady state of the temporal dynamic is just stochastically defined. There is a bias for the first percept being a long, persistent grouped perception. Both sensory modalities have the same switching mechanisms controlling them. During bistable visual stimulus, competition has been observed in V1 in Binocular Rivalry (Tong et al., 1998) and in other types of visual ambiguous stimuli (Murray et al., 2002), as well in neuronal populations coding for specific attributes involved in the competition (Moutoussis et al., 2005). A study that used MEG found that segregated perception was associated with larger long-latency potentials for B tones (Gutschalk et al., 2005), thought to be created in non-primary auditory areas. The neural responses to ABA sequences decrease during the presentation, but the time constants are different for A and B tones (Micheyl et al., 2005). These stimuli have some similar features and likely involve competition at distinct levels of the central nervous system (Pressnitzer and Hupe, 2006).

Einhauser et al (2019) made a study combining auditory streaming and visual plaids to compare various types of multistable stimuli and they used measures such as the dominance of percepts and the total number of perceptual reversals, in order to compare the performances between stimuli with different characteristics. This study proposes that a subject's number of perceptual reversals in a visual plaid has a significant correlation with the number of transitions in auditory streaming. Moreover, individuals that have a stronger tendency to perceive the auditory streaming stimulus as integrated also have the same tendency in the visual stimulus. Conceptually, when the presentation duration of a stimulus is short, it can cause more outliers in any measure of dominance (Levelt, 1967, Zhou et al., 2004). This can lead to smaller correlations when comparisons are made with studies that used long duration (Einhauser et al., 2019). Correlations between both modalities of phenomena were found, instead of what happened with Pressnitzer and Hupe (2006), Denham et al (2018) and Kondo et al (2018) (They only said the similarities exist). Different forms of multistability have common supramodal mechanisms and similar physiological effects (Einhauser et al., 2008, Hupe et al., 2009) or similar regions in the brain that are involved in the resolution of conflicts caused by various multistable stimuli (Sterzer and Kleinschmidt, 2007).

2.3. Brain oscillations in multistability and bistability

Bistable stimuli have been used to study mechanisms of perceptual inference and have shown that brain oscillations have different behaviours during a stable moment of perception and moments of perceptual reversal (Zaretskaya and Bartels, 2015). However, it is still uncertain the role of oscillations in the beta band during bistable and multistable perception.

The Necker cube was used as visual stimuli by Isoglu-Alkac et al (2000) and they compared the alpha band (8-12Hz) before the perceptual changes during the experiment. A decrease in alpha activity was found prior to a perceptual reversal but not immediately prior or during the report. After that, another study with the same characteristics found this same decrease in the lower alpha band (6 – 10 Hz) power (Isoglu-Alkac and Struber, 2006). Struber and Herrmann (2002) studied alpha band activity during perceptual transitions in MEG using two types of reversals. Exogenous reversals occur when there is a change in the stimuli and endogenous reversals take place when the alternation of the percept occurs during the presentation of a constant ambiguous stimuli (Struber and Herrmann, 2002). If the reversal was exogenous, alpha activity decreases between 300 and 200 msec before the reversal is reported. In the case of endogenous reversals, the decrease in alpha occurs 1000 msec prior the change of perception (Struber and Herrmann, 2002), which can indicate there is a change in the behaviour of brain oscillations during perceptual reversals. Another study from Basar-Eroglu et al (1996), found that gamma band activity (30 - 50Hz) were dominant in the right frontal cortex within 1000 msec prior to the report of percept reversal.

Van Rullen et al (2006) studied the mechanisms underlying illusory motion reversal (IMR) and they found that the power of the oscillations with 13Hz of frequency increased before transitions between illusory and real motion percept and decreased after transitions between real and illusory motion percept.

Okazaki et al (2008) used a figure-ground bistable image with two different possible interpretations, namely “face” or “saxophone” (see figure 1.4B) and unambiguous alternatives eliciting either of the two interpretations. Two conditions of stimulus and perceptual change were created, one with the face image shown first and the ambiguous image after (F-T condition), and another task with the saxophone image shown prior to the ambiguous picture (S-T condition). The face interpretation was considered dominant, independently of the preceding picture. There were more perceptual transitions in the S-T condition, and it was found that after perceptual reversals there was a greater activity in beta band oscillations in occipital and parietal regions in this S-T condition than during F-T condition. This suggests that there is a burst of beta oscillations after the alternations for a dominant percept.

Piantoni (2010) focused on a similar stimulus as VanRullen et al (2006) that produced illusory motion reversal (IMR) and compared it with BR, where two different images are presented each to one eye (Quinn and Arnold, 2010). In both stimuli, there were large changes in the activity of beta band oscillations during perceptual reversals. The power of beta oscillations during the real motion percept was higher than this power during illusory motion percept. As the percept moving in the direction of the real motion is the first perceived and the one perceived for the majority of time, it is possible to say that beta band activity is higher during the dominant percept. In the case of the BR stimulus, the probability of each percept is of 50% and the activity of beta band oscillations does not have significantly alterations.

Minami et al (2014) studied insight problems, where there is a moment of clarification, either if it is a difficult problem to solve or an ambiguous stimulus. This study presented to subjects hidden figures and ambiguous grey images. It was noticed that the power of beta oscillations decreases during perceptual reversals in parietal-posterior regions, which supports the theory that beta-band activity is related to the maintenance of the *status quo* and the transition of the cognitive state.

Another study, by Zaretskaya and Bartels(2015), used a bistable stimulus with local motion perception and global motion percept. When the subjects reported global perception, the power of the beta band was lower than when they reported local percepts. These differences were located in the posterior parietal cortex. While the findings support a role for beta in the integration of motion, which is how the authors interpreted the findings, this could also result from an imbalanced bistability. In fact, beta was correlated with the local motion which also happens to be the first configuration perceived, likely the default perception. Hence, one can also interpret this data not as evidence for a role in motion integration but perhaps as a signal of default or dominant interpretations of an ambiguous stimulus.

Costa et al (2017) studied how the brain integrates the information for distant areas of the visual brain, in an effort to identify mechanisms of binding in the so-called “binding problem”. The study employed an ambiguous stimulus involving motion bistability while an EEG was recorded. The results showed that different perceptual interpretations were related with changes in beta power, that was increased during bound perception relative to a segregated perception and came mostly from parietal regions.

2.4. Goals

This project has a primary goal of studying ambiguous stimuli, one visual and one auditory, and being able to bias them to one interpretation becomes dominant over the other. After this, the main goal of this project is to study the brain oscillations and find if, in ambiguous perception, beta activity increases when the dominant percept is perceived and if it decreases when the alternative percept is the one interpreted.

3. METHODS

In this chapter is presented the methodology used during the experimental part of this work. This study is divided in two major areas, psychophysical and electroencephalogram parts, and this chapters presents the methods for both of them.

3.1. Participants

Fourteen subjects were recruited for the present study. Seven of the participants were female and all subjects were within 20 to 35 years old. Two of them were researchers of this study (GACO and MASA) and the others were graduate or undergraduate students, naive to the purpose of the experiment. All of them were healthy and had normal or corrected-to-normal vision. Prior to participation all of them gave written informed consent. Thirteen of the observers were right-handed with laterality index between 75-100 according to the Edinburgh Handedness Test (Oldfield, 1971) with only one considered middle, with a score of 20 in the same test (MAPA). All the participants were able to perceive both configurations of each stimulus and were first accustomed to the stimuli before starting the calibration. All of them performed the calibration part and electroencephalogram part of the experiment except for two (ROAB and AIIN) which only participated in the pilot studies

3.2. Visual Stimulus

The Stroboscopic Alternative Motion (SAM), also known as Bistable Motion Quartet, is an ambiguous stimulus that is commonly studied in bistable vision (Chaudhuri and Glaser, 1991, Genc et al., 2011, Schneider et al., 2019). The visual stimulus was created in MATLAB (The MathWorks, Inc., Natick, MA) using the Psychophysics Toolbox (Brainard, 1997). Visual stimulation for both the calibration and the EEG experiment was displayed on an LCD monitor with a refresh rate of 60Hz and with dimensions of 33 x 62.5 cm and resolution of 1920 x 1080 pixels at a distance of 55 to 70 cm from the subject. The stimulus was adapted so that its scaling adjusted to the distance from the subject to the monitor. The stimulus consisted in four flashing dots arranged in a rectangular configuration.

Only two dots were shown at a time in diametrically opposing vertices. Each set of two dots was displayed for 184 msec with an Inter Stimulus Interval (ISI) of 67 msec where no dots were shown before the next pair was shown. After the ISI the other set of dots was presented in the same way followed by an ISI after which the cycle was repeated. Figure 2.1A shows the positions of the dots in the two alternating states. From the onset of one frame to the onset of the next 250 msec elapsed, meaning a full cycle of onset-to-onset of frame 1, with one frame 2 presented and two ISIs in between, was completed every 500 msec. This results in a stimulus frequency of 2Hz, i.e. 2 full cycles as defined above every second. Each dot had a diameter of 1° of visual angle diameter and the square shape comprised of the positions where dots could be displayed (i.e. the square's vertices) was 5° x 5° visual angles (*w* x *h*). For the purposes of the present study, the above described figure's vertical and horizontal dimensions were increased or decrease to produce a stimulus with a more rectangular shape as will be described further. In the case of the square it will have a ratio of 1, i.e. the length of the horizontal dimension divided by the vertical, with width and height of the same size, while rectangular configurations will have a ratio smaller or larger than 1. This stimulus produces a strong perception of motion, despite the dots not moving between frames but only being flashed in distinct positions. For this reason, this type of motion is referred to as apparent motion. It is an effect similar to beta motion (Robinson, 1972) but in this case it is also ambiguous since the stroboscopic two pair of dots can be displaced in either a vertical or horizontal orientation in order to describe a transition from frame 1 to frame 2 (Figure 2.1B). A fixed red cross was also present during the entire stimulus presentation for the subject to direct their eyes to. This stimulus was used in both parts of the study.

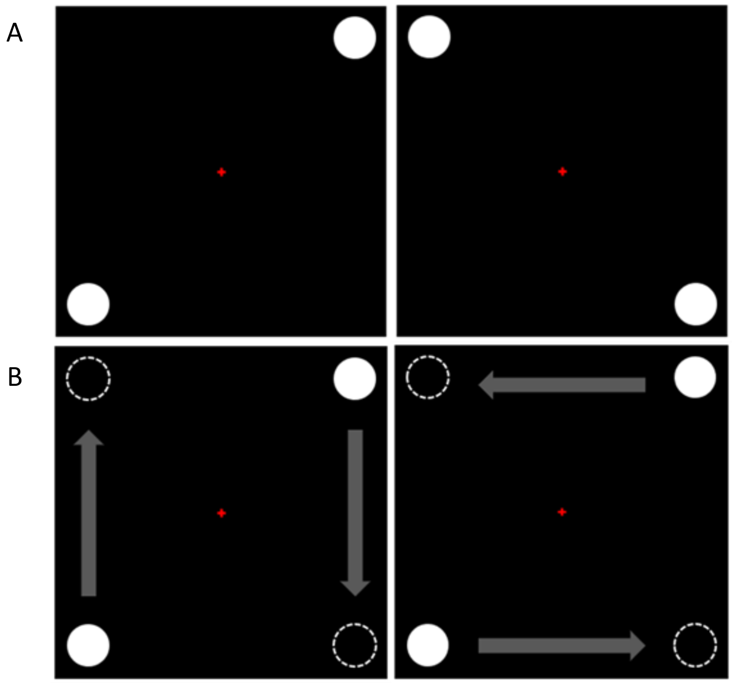

Figure 3.1 Stroboscopic Alternative Motion or the "motion quartet". A) The SAM stimulus consisted of two frames that alternated in succession creating a strong perception of motion. B) Apparent motion could be perceived in either a vertical or horizontal direction (arrows).

3.3. Auditory Stimulus

The auditory stimulus was generated in MATLAB (The MathWorks, Inc., Natick, MA) using the Psychophysics Toolbox (Brainard, 1997). Several studies have reported auditory stimulus that can also be perceived in two different ways and that share several of the common features of bistable percepts (Noorden, 1975). This is possible with a stream of 2 simples tones presented in succession, usually referred to as auditory stream or an "ABA_" stream paradigm (Gutschalk et al., 2005, Pressnitzer and Hupe, 2006, Kondo and Kashino, 2009, Billig et al., 2018, Curtu et al., 2019). This ambiguous stimulus will be referred as ABA from now on. Its bistability emerges as sometimes the sound is perceived as a single "chunk" of tones corresponding to ABA triplets, creating a perception of only one stream of sound. In other moments, the sound is perceived as two separated streams, one composed of A tones and the other of B tones, the latter with a rate half of the former. Each triplet is a sequence of a high tone (A), a low tone (B) and another high tone (A), each of them has a duration of 100 msec. Between tones there is an Inter Tone Interval (ITI) of 50 msec and between triplet there is an ISI of 200 msec. In the current setting the bass frequency (tone B) was kept at a fixed value of 1000Hz, while the high frequency tone (A) varied in a number of semitones (*st*) above frequency of tone B. The tones had a cosine ramp up and down of 10 msec combined, adapted from stimuli from the Psychoacoustics toolbox (Soranzo and Grassi, 2017). The stimulus stimulus consists in a sequence of such ABA_triplets presented diotically at 65dB, using Sennheiser headphones (HD 280 Pro). A fixed red cross was constantly displayed in the monitor for the subject to maintain fixation, as in the visual task, and reduce distractions. In the task the observer must report continuously which perception he/she is currently perceiving during a trial of a few minutes.

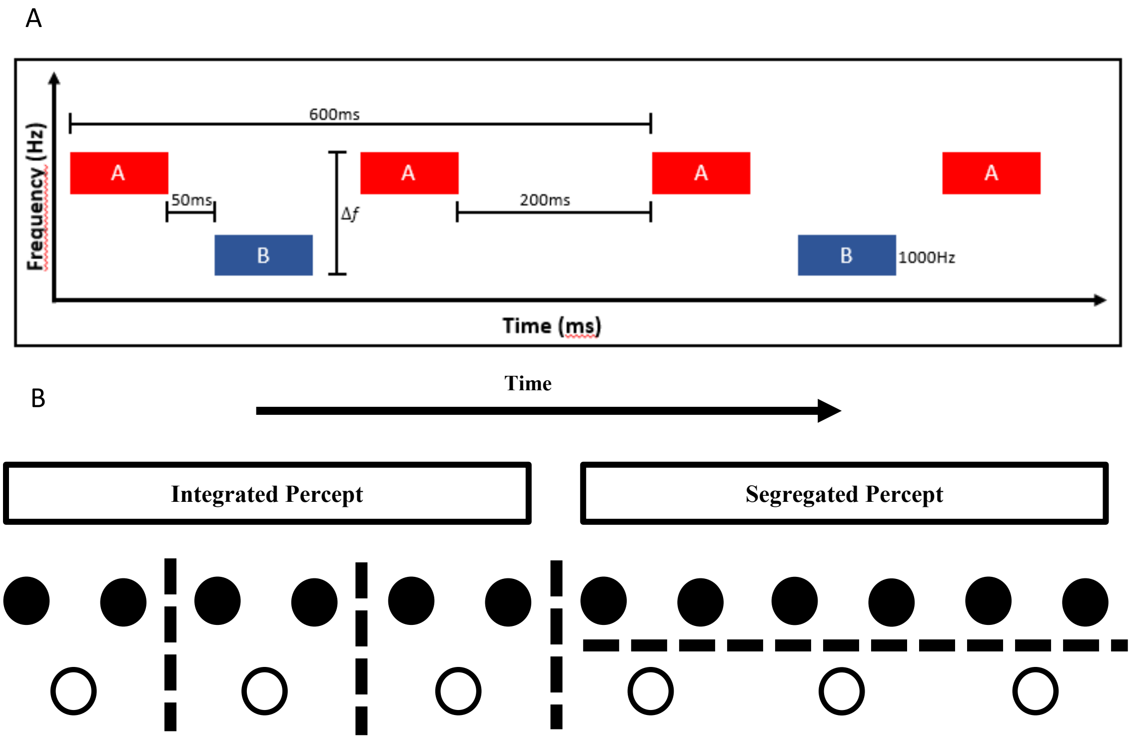

Figure 3.2. Bistable auditory stimulus. A) Scheme of the auditory stimulus used in the auditory task. A and B tones were separated by an inter-tone interval and triplets were separated by a longer inter-stimulus interval corresponding to a duration of a single tone plus two inter-tone intervals. B) Visual depiction of the two possible perceptions from the ABA_ Paradigm.

The difference in sound frequency between the two tones (f_x, f_y) was calculated using the following formula for a semitone (*st*) difference relative to a frequency (f_x) (Kügler et al., 2009):

$$st = 12 \times \log_2\left(\frac{f_y(Hz)}{f_x(Hz)}\right) \tag{3.1}$$

If the formula is rearranged for the incognita to be the frequency of the tone (f_y) that is a certain number of semitone (st) apart from the frequency of the other tone(f_x)

$$f_y = f_x \times 1.0595^{st} \tag{3.2}$$

This stimulus, with parameters as detailed above, was used in the final behavioural and EEG study. Nonetheless, a series of pilots with different parameters was first tested. The details of these stimuli can be found in section 4.1.

3.4. Ambiguous Stimuli Calibration

The first part of the experiment consisted in the calibration of certain parameters of each stimulus. In this sub-section we explain all methods used in this initial part of the study.

3.4.1. Determining individuals' parity ratio

SAM is an ambiguous stimulus that leads to two different perceptions of motion, as previously said. When the dots are equidistant over horizontal and vertical distances, a width/height ratio of 1, most observers are more likely to perceive vertical motion (Genc et al., 2011). This asymmetry happens when the stimulus is visualized in central fixation and is attributed to the cost of integration across hemispheres when motion is perceived horizontally (the dots "switch" from one hemisphere to the other) , while vertical motion perception requires just intrahemispheric processing (Chaudhuri and Glaser, 1991). This visual stimulus provides optimal conditions to study the role of brain oscillations related to perception and disambiguation of bistable stimuli (Kornmeier and Bach, 2012), as will be detailed later. As stated before, it has been suggested by Piantoni et al (2010) that beta oscillations might underly neuronal mechanisms related to perceptual dominance under ambiguity. The authors mainly propose that beta oscillations correlate with the perception of the more probable percept when the brain is faced with ambiguity and two or more alternative perceptual configurations are possible. In order to explore this hypothesis, it was set to devise a stimulation paradigm that could be easily biased toward one of two different percepts with minimal changes to the essential content of the stimulus. SAM was selected as the ambiguous stimulus for this task as it can easily be biased by a simple change in the figure’s proportions (Chaudhuri and Glaser, 1991). Hence, in order to guarantee that the stimulus was properly biased to influence the observer towards one percept more frequently than the other, i.e. having a dominance of one percept over the alternative, the Parity Ratio (PR) of each volunteer had to be found. PR is the ratio of the vertical and horizontal distances of the dots in which the observer has a probability of 50% of perceiving vertical motion and a probability of 50% of perceiving horizontal motion. This measure is intrinsic and different for each person. To find this ratio of equiprobable perception and further manipulate the stimulus towards biased versions, a methodology previously used by Genç et al (2011) was employed. In this work, two standard methods in psychophysics were applied in combination to find PR: first the Method of Limits and second the Method of Constant Stimuli.

- **Method of Limits**

The Method of Limits (MoL) is one of the classical psychophysical tools. In this method a value in the stimulus is varied from trial to trial until the volunteer reports a change in perception. MoL is performed in two phases, the ascending phase and the descending phase, with the stimulus’ parameters being varied in opposite ways. In the ascending phase, the value to be changed such as contrast starts a minimal level and is increased gradually until it reaches a threshold where the subject is able to detect or perceive it. Likewise, during descending phase, that same parameter will be set to a maximum where perception is certain and is decreased gradually until the observer perception changes, for instance the subject stops perceiving the stimulus. Usually, both phases are used in psychometric experiences and the average of all end values is used to estimate the threshold, i.e. the point where there is a switch in perception or performance. It is a simple method to apply, but it has its shortcoming that can lead to two types of errors. First, due to a continuous stimulation and gradual change in the stimulus the observer might not perceive a change at values near the threshold as determined by short presentations for instance, an effect mainly ascribed to adaptation mechanisms and hystheresis. Second, the observer may anticipate the change of the perception before the threshold leading to an overestimated detection threshold. (Lu and Dosher, 2014)

- **Method of Constant Stimuli**

The Method of Constant Stimuli (MoCS) measures the performance of an observer during the task with the characteristics of the stimuli constant over a range of different values. Then, the threshold is obtained using a psychometric function that relates performance to stimulus variation. The values of the stimuli are chosen randomly from preselected values ranging over values that fall on maximal and minimal levels of performance, be it of stimulus detection or, as in the current project, of maximal and minimal perception of a current perceptual configuration. The subject reports their perception for several runs and the probabilities of the answers for the set of stimulus values are used to fit the psychometric function. In most instances the threshold, e.g. 50% for a threshold of "above chance level" or in the current case the PR, has to be interpolated as the measured performance over preselected values will rarely happen to fall in the subjects threshold. (Lu and Dosher, 2014)

3.4.2. Visual Task – SAM calibration

The observers had to do a run for MoL and then MoCS was performed. The MoL of the visual stimulus was a set of 40 trials, 20 for the descending phase and 20 for the ascending phase in random order. The stimulus SAM where the white circles were shown as in figure 3.1. The dots had 1º of visual angle diameter. During one ascending phase, the ratio started at 0.25 (ratio width/height, i.e. the length of the vertical dimension is four times bigger than the length of the horizontal dimension) making the subject start the trial perceiving the circles in horizontal apparent motion and it is gradually increased until the subject reports a perceptual change or it reaches the ratio of 4, ending the trial. During the descending phase, the ratio starts at 4 (width/height = 4), making the observer perceive the circles displacing vertically, and it is gradually decreased until the perception changes or it reaches the ratio of 0.25. When the ratio is 1 the horizontal and vertical dimension have both 5º, in visual angles. In each trial one of the two phases starts and the observer must report their perception of the dots motion, by pressing either of two buttons on a keyboard, depending on the perceived motion: button 1 for vertical motion; and button 2 for horizontal motion. The observer must report the perception uninterruptedly, i.e. holding the button down, as soon as they are certain of the currently perceived configuration. When perception changes to the other possible configuration, due to the gradual change in the stimulus' ratio, the subject was instructed to press the button corresponding to the new configuration. Afterwards, the current trial immediately ends and the next one is ready to start as soon as the subject decided he was ready. MoL finishes after the 40 trials are performed. The estimated PR for each participant was obtained by averaging all ratios where participants reported the perceptual switch.

The current stimulus was further adapted, compared to previous studies (Chaudhuri and Glaser, 1991, Gilroy et al., 2001, Genc et al., 2011), one of the dimensions is kept constant, while the other varies, being increased or decreased if it was an ascending phase or a descending phase, respectively. This method of changing the relative vertical and horizontal distances of the dots produces the effect of biasing perception towards vertical or horizontal motion, as expected, but leads to a change in the stimulus' scaling, since the area will increase or decrease with the expansion of one of its dimensions. In the settings and experimental conditions of the current study, using a similar approach with a ratio of 0.25 for instance would lead to a stimulus where the circles fall at the margins of the subject's peripheral vision. In fact, the dots almost did not fit in a regular computer monitor and, in the acquisition monitor, they were too far apart. To maintain the stimulus centred and to not force the observer to use peripheric vision, it was decided to maintain the area of the configuration rectangle constant. In this way, in each step both height and width changed its size in opposite directions, meaning, if the height increases width decreases. After each trial, the ratio in which the switch of perception occurred was registered and, in the end, the average of those ratios corresponded to the first PR.

In both parts there is an incremental step that increases or decreases the logarithm of 10 of the ratio in the corresponding part (in an ascending phase the ratio increases, and in a descending phase the ratio decreases). The incremental step was calculated as follows:

$$I_{step} = \frac{\log_{10}(R_{max}) - \log_{10}(R_{min})}{n} \tag{3.3}$$

Where, R_{max} is the starting ratio of the descending part, R_{min} is the starting ratio of the ascending part and n is the number of steps, which was set to 80.

The logarithm was used in the step to iteratively increment or subtract the ratio. This happened taking into account the following example. A rectangle of length (x) of 2.5 and height (y) of 10 corresponds to a stimulus in one extreme of the width/height ratio with a ratio of 0.25, meaning the stimulus in the opposite extreme must have a length of 10 and height of 2.5, which correspond to a ratio of 4. Comparing the values, it is possible to notice that starting at a ratio of 1 (i.e. the dots' positions fall on the vertices of a square) it takes 12 increments of 0.25 to reach the ratio of 4 (e.g. 1.25, 1.5, 1.75… up to 4) while a reduction of only 3 steps to get from 1 to a ratio of 0.25 (e.g. 0.75, 0.5, 0.25), which corresponds to the stimulus with opposite proportion (a ratio of 4 corresponds to a stimulus 4 times as wide as it is tall while a ratio of 0.25 describes a stimulus 4 times as tall as it wide, in essence one image is a 90º rotated version of the other). To be sure, working on a linear scale and changing the ratio by a fixed value does not produce stimuli that are a rotated version of each other. However, if the value of the ratio is converted to logarithm, it is already possible to subtract and add the same value and have a fair increase and decrease of the ratio and produce a range of stimuli that are symmetrical around the ratio of 1. Taking the same previous example, a ratio of 0.25 corresponds to the value -0.6021 after the logarithm, and the ratio of 4 corresponds to the value 0.6021 after the logarithm. Both are 0.6021 apart from the 0 which is the logarithm of 1. Therefore, the incremental steps were defined as the logarithm of the ratio. After that, the antilog is made to obtain the value of the ratio.

With PR value obtained for each volunteer, the set of eight ratios to be tested during MoCS can be computed. One of them was the PR estimated in the method of limits and the other seven were around this value, with three of them selected below and the other four above PR. Every point was apart 0.08 to the logarithm of the ratio of the previous one. In this second part of the calibration, each volunteer had to do the task twice for each different ratio, resulting in 16 trials of 3 min each. During these trials, the task is the same as before, but parameters are kept constant and hence SAM does not change its aspect ratio. Participants reported their perception by pressing one of two buttons as before, referring to vertical and horizontal motion, but contrary to the MoL task the trial did not end when a switch was perceived. Hence several perceptual switches occurred during a 3 min trial and the duration of each perceptual state was recorded. The percentage of dominance of vertical motion perception for each trial was calculated based on the subject's responses.

3.4.3. Auditory Task – ABA calibration

As previously described, the stimulus chosen was the *ABA_ Paradigm*. The characteristics used were, ISI of 200 msec, ITI of 50 msec, tone duration of 100 msec, frequency of tone B constant and equal to 1000Hz, as reported before. Each volunteer had to respond to 16 runs of 3 min, with each of the 8 semitone differences being tested twice. The following semitone differences were tested: 1, 2, 3, 6, 9, 12, 16 and 22. The frequency of tone A was set to x semitones above the frequency of tone B.

Similarly, as with the SAM task, when the subject perceives the sound as integrated, they are instructed to press the button 1 continuously as long as that percept holds, and when perceiving the sound as segregated subjects were to press the button 2. All the volunteers were informed that in a moment of confusion or indecision they could release any button until they understand clearly which perception they are having. Based on the duration of perception of each of the two configurations, the percentage of dominance of segregated perception for each trial was calculated.

3.4.4. Psychometric Functions

After the MoCS, psychometric curves must be fitted to individual subject performance to find the points of 35% and 65% dominance of vertical motion percept for the visual task and the points of 35% and 65% dominance of segregated percept for the auditory task. These values will be used in the EEG part of the experiment. The psychometric functions were obtained using the Palamedes toolbox from Matlab (Prins and Kingdom, 2018). This toolbox employs a method to fit data to Psychometric Functions (PF). The method used by the toolbox iteratively look over a variety of possible values of two parameters, α and β. The first one defines the general position of the function along the axis of the abscissa. In the case of the Logistic function, α corresponds to the point in the abscissa with 50% dominance. The parameter β refers to the slope of the curve. The fitting procedure does not find their exact value, nonetheless it estimates their value that generate a curve capable of best match the psychophysical data. There are still two more parameters the ϒ and the λ. The first parameter is the guessing rate and describes chance-level performance. It is the percentage of correct answers that can result from simple guessing. In the case of the experiments of this work, there is no right or wrong answer, and it is useful to define the value of the parameter ϒ = 0. The parameter λ is the lapse rate and accounts to trials that the observer may miss or not being attentive and consequently produce an incorrect answer. In the case of these experiments as, once again, there is no right or wrong answer, the lapse rate is 0. Usually, this parameter is considered 0 and if in some researches there is a suspicion of lapse, the value of λ can be 0.01. These two parameters are "fixed parameters", because they do not change during the fitting procedure. In opposite to this, α and β are "free parameters" due to their variation during the fitting. The method used was the Maximum Likelihood criterion, where the psychometric function defined is the one that better recreate the experiment as if it was completed by a human observer. To evaluate the goodness-of-fit of the curves, it is calculated the deviance and its correspondent p-value. (Kingdom and Prins, 2010)

Two types of psychometric functions were used, Logistic and Weibull, for visual and auditory tasks, respectively. Their equation is presented next (Kingdom and Prins, 2010):

- Logistic Function (F_L)

$$F_L(x;\alpha,\beta) = \frac{1}{1+\ e^{(-\beta(x-\alpha))}} \tag{3.4}$$

- Weibull Function (F_W)

$$F_W(x;\alpha,\beta) = 1 - e^{\left(-\left(\frac{x}{\alpha}\right)^{\beta}\right)} \tag{3.5}$$

As the psychometric curves are used in the calibration of this work to find some stimulus levels that result in a certain performance, formulas for each type of function used to fit the data are presented below:

- Logistic Function (F_L)

$$x = \frac{\log_{10}(-\ln(1 - F_L(x;\alpha,\beta)))}{\beta} + \ \alpha \tag{3.6}$$

- Weibull Function (F_W)

$$x = \alpha \times \sqrt[\beta]{-\ln(1-y)} \qquad (3.7)$$

3.4.5. Unambiguous visual stimulus

In addition to the two stimuli mentioned earlier, the participants had to respond to an unambiguous visual stimulus in the EEG part of the experiment. This was decided because the beta signal to analyse, is believed to relate to the brain activity taking a decision from an ambiguous stimulus. Given the nature of the task it is possible to have confounds, for instance motor activity and attention. In this way, it was used an unambiguous visual stimulus, similar to SAM. In this stimulus there is no ambiguity whether on the perception is vertical or horizontal. The dots reproduce the same motion as reported by the subject in the ambiguous version performed immediately prior. For instance, if a subject reports 5 sec vertical motion and then 10 sec horizontal motion, in the unambiguous stimulus it will show to the subject 5 sec of vertical motion and then 10 sec of horizontal motion. In this stimulus, the configuration of the stimulus areas and the dots positions describe a square of 5º x 5º visual angles, meaning the unambiguous stimulus has a ratio of 1. A scheme of this stimuli is shown next.

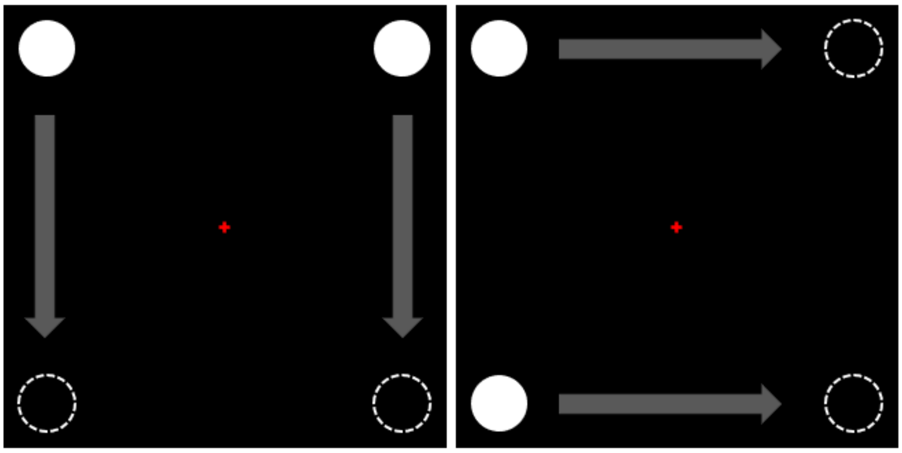

Figure 3.3 Unambiguous visual stimulus. Both perceptions of the unambiguous visual stimulus.

3.5. EEG Recording and Analysis

In the second part of the experiment, the EEG was acquired while the subject had to perform the psychophysical tasks. In this sub-section all the methods of this part of the study are described.

3.5.1. Procedure

The testing conditions were adapted for each subject by adjusting the aspect ratio of the stimulus in SAM, the ones estimated in the psychometric curves that corresponded to the points of 35% and 65% dominance of vertical motion. Likewise, semitone difference used in the ABA task corresponds to the points of 35% and 65% of segregated perception estimated in the psychometric functions obtained in the calibration of the auditory task.

If a 35% dominance corresponds to an extrapolated value, i.e. matching the psychometric fit but outside of the range of points used in the calibration, the lowest aspect ratio/semitone difference tested during MoCS was used. As well, if a 65% dominance falls above the MoCS range, it was used the highest aspect ratio/semitone difference tested during MoCS.

The visual task consisted of runs of 3 minutes performing the ambiguous and unambiguous stimulus. Each subject had to perform 2 runs of the ambiguous stimulus for each hand and for each aspect ratio computed in the calibration part (35% and 65% dominance of the vertical motion percept). After a run of ambiguity, the observer had to perform a run of the unambiguous stimulus, where the unambiguous task recreates the conditions based on the prior ambiguous answers, as explained above.

The auditory task consisted of runs of 3 min and each subject had to perform 2 runs for each hand and for each semitone difference computed in the calibration part (35% and 65% dominance of the segregated percept). Every subject selected for both tasks, performed the visual task, SAM, first, except for one that preferred to perform the auditory task first. Both hands were used in the same number of runs to avoid confound related with the motor activity.

3.5.2. EEG Acquisition

EEG signal was recorded using a 64-channels NeuroScan QuikCap with 60 Ag/AgCL electroned that were positioned in agreement with the extended 10-20 system and to which four channels were added, for vertical and horizontal EOG. The data was acquired using the software Scan4.5 Acquisition Software (Compumedics Inc, Singen, Germany). The electrode impedances were maintained below 10 kΩ during the acquisition and when the signal looked noisy this was checked. EEG data was continuously recorded during each run and triggers were sent and registered in the signal. These triggers concern the beginning and the end of the run, the button press when there is a change in perception and the information of the change of the dots in the visual task. The signal was amplified, it was applied a low pass filter at 200Hz, and it was digitalized at 1000Hz. EEG signal was recording while the subject performed the psychophysical tasks.

3.5.3. Pre-processing

EEG data was pre-processed before the frequency analyses were made. For this, pre-processing was performed offline using MATLAB and FieldTrip toolbox (Oostenveld et al., 2011). In the beginning all data was epoched according to the position of the triggers as times of interest. There were two types of epochs, non-time locked (nonTL) or time locked (TL). The first is regarding the moments when there is no perceptual reversal by the participant but instead perception is stable. In both experiment, there were two conditions nonTL, one for each percept of the ambiguous stimulus. These epochs have 1 sec in length and start one second after the trigger of a perceptual reversal and stop one second before the trigger of the next perceptual reversal. Two padding segments of 0.5 sec before and after the epoch. The second set of epochs corresponded to the moments of the EEG signal where there was a trigger of perceptual reversal. As well as in the other type of epochs, there were two conditions TL, one for each percept of the ambiguous stimulus. These epochs have 3s of length and start 1.5s before the trigger of perceptual reversal and end 1.5s later the same trigger. Two paddings were also added, 0.5s before the epoch and 0.5s after the epoch.

All data was bandpass filtered (1-100Hz, finite impulse response (FIR) filter) and some channels were removed (M1, M2). After that, all channels were re-referenced to the average of all scalp electrodes, excluding the VEO channel. Epochs containing artifacts (e.g. electrode pops, swallowing, muscular movements) were removed by visual inspection. In case of the presence of bad channels, they were removed. After that, data was appended according to the type of epochs and the stimulus. The next step was performing an Independent Component Analysis (ICA) to all datasets. ICA consists of searching for a linear transformation that reduces to the minimum how components statistically depend on each other (Comon, 1994). Every component representing eye movements and blinks, identified by their scalp topography and spectra, was removed. In the end, removed channels were interpolated using spherical spline interpolation (Perrin et al., 1989).

3.5.4. Frequency Analysis

In frequency analysis, power spectrum is computed for nonTL epochs for each perceptual condition. It was used Welch’s periodogram method for estimating power spectrum. This method is carried out by dividing the epochs into overlapping blocks, forming the periodogram for each block (Welch, 1967) and each of them was Hanning windowed. A fast Fourier transform (FFT) was applied in each block. The FieldTrip toolbox was used for this analysis, as well.

3.5.5. Time Frequency Analysis

In order to analyse event-related spectral changes, it was performed time frequency analysis over epochs of TL condition, which means, in epoch with a perceptual reversal. There are two ways to perform this analysis, either the time window has always the same length independently of the frequency, or the time window decreases its length with the increasing of frequency. It was decided to use the second method in order to prevent the loss of resolution in higher frequencies. It was used the Welch’s periodogram method and a Hanning window, as well, but instead of an FFT, it was used an adaptive Morlet wavelet (initial 3 cycles for 6 Hz). This method has an increasing number of cycles with the increasing of frequency, which works as a trade-off to balance resolution in frequency and resolution in time through the spectrum. The FieldTrip toolbox was used for this analysis, as well.

4. RESULTS AND DISCUSSION

In this section of the present work, the results are presented and discussed. In the beginning the results for the first and second pilots made for the auditory stimulus are presented. Next, the psychophysical results from the calibration part of both tasks are shown and described. The psychophysical results of the EEG part of the experiment follow psychophysical results from the calibration task. In the end, the analysis made to the EEG data acquired are presented and debated.

4.1. Auditory stimulus pilots

As the quantity of ambiguous auditory stimulus using auditory streaming with different characteristics is high, it was needed to perform two pilot experiments to decide some of the characteristics of the stimulus to be used in the experiment.

4.1.1. First pilot

As mentioned before, several studies have used this particular auditory stimulus, i.e. strains of "ABA_" tones, but the frequency of tones and other parameters of the stimulus often differ. To choose those that would make it more suitable for our experiment, i.e. with an adequate reversal rate and subject to being biased, a pilot was created and tested by 4 participants (two are researchers in this study). In the pilot study three variants of the auditory bistable stimuli were used. These consisted of stimuli with different base tones, different tone duration and different intertone interval, reproduced according to auditory stimuli reported in Curtu et al(2019), Pressnitzer and Hupe (2006) and Kondo and Kashino (2009), referred to stimulus A, B and C from now on, respectively (see Table 4.1). The pilot task consisted of seven three-minute runs (following a stimulation protocol as much as possible similar to the visual task, see Methods and section 4.2 and also Costa et al 2017) for each one of the three different stimuli. In a group of 7 runs what varied between conditions is the semitone difference between the frequencies of tone A and tone B, in the same way the visual stimulus had the ratio of the vertical and horizontal distances varying. A semitone is the smallest musical interval (Kügler et al., 2009) and was here the smallest distance between two consecutive notes (fractions of semitone are possible but were not employed here). The pilot was made with semitone differences of 1, 3, 5, 7, 9, 12 and 16.

In the table 4.1 are specified the characteristics of each auditory stimulus used in the first pilot for the auditory ambiguity perception.

Table 4.1. Characteristics of the3 stimuli tested in the first auditory pilot.

Stimuli/Characteristics	Tone A (Hz)	Tone B (Hz)	ISI (ms)	ITI (ms)	Tone duration (ms)
A *(Curtu et al., 2019)*	1123 (1000 + 2st) or 1415 (1000 + 6st) or 1588 (1000 + 8st) or 2001 (1000 + 12st)	1000	200	50	100
B *(Pressnitzer and Hupe, 2006)*	587 (440 + 5st)	440	120	2	120
C *(Kondo and Kashino, 2009)*	1060 (1000 + 1st) or 1189 (1000 + 3st)	944 (1000 – 1st) or 841 (1000 - 3st)	160	60	4

Figure 4.1 and 4.2 show the results of the first pilot performed, that is, the ratio of time during the task that the observer reports perceiving the sound segregated as a function of semitone difference between frequency A and frequency B and the number of switches per minute, henceforth referred to as reversal rate, per semitone difference, respectively. Each graph shows the results for three to four subjects for each stimulus. The participant AIIN only performed the task with stimulus A and C as stimulus B had already been considerable to be nonviable for the purposes of this study with the first three subject (detailed further).

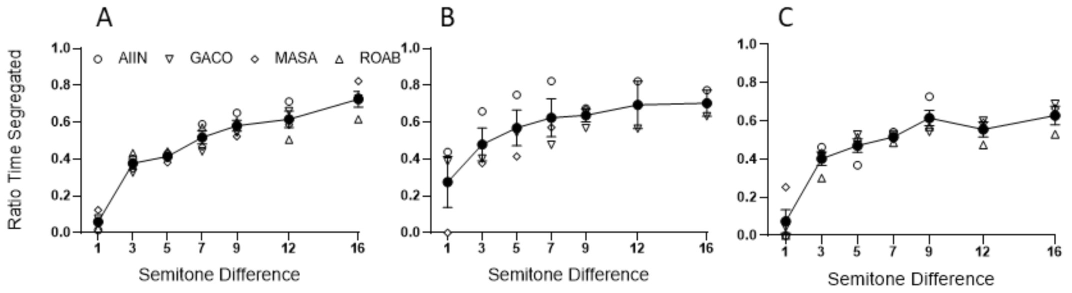

Figure 4.1. Ratio of time during the task that the observer reports perceiving the sound segregated as a function of the semitone difference between tone A and tone B. A) Results of the auditory task using the characteristics of the stimulus A. B) Results of the auditory task using the characteristics of the stimulus B. C) Results of the auditory task using the characteristics of the stimulus C.

Analysing the relative dominance of the two percepts (Figure 4.1), all stimuli showed a positive correlation between semitone difference and the duration of segregated perception: the higher the semitone difference the longer the perception of two segregated streams (two-way repeated measures ANOVA, main effect semitone difference: $p < 0.0001$ for stimulus A; $p = 0.0002$ for stimulus B; $p = 0.0014$ for stimulus C). For all stimuli conditions tested over a range of semitone differences (1, 3, 5, 7, 9, 12 and 16 semitones) conditions which favoured a grouped/triplet perception (conditions with mean segregated perception below 0.5) or a segregated/streaming perception (above 0.5) were found. For stimulus A the relative segregated perception varies from 0.060 ± 0.051 for 1 semitone difference to 0.726 ± 0.085 for the 16 semitone difference, while for stimulus B these values range from 0.275 ± 0.240 for the small semitone difference to 0.704 ± 0.100 for the high semitone difference and for stimulus C from 0.074 ± 0.121 to 0.628 ± 0.086 for the two conditions respectively. Since the current study aims on exploring variations on the parameters of similar bistable stimuli to produce a varying dominance of percepts, from this brief analysis one can appreciate that stimulus A results in a better psychometric function across subjects and is thus a better candidate for the study.

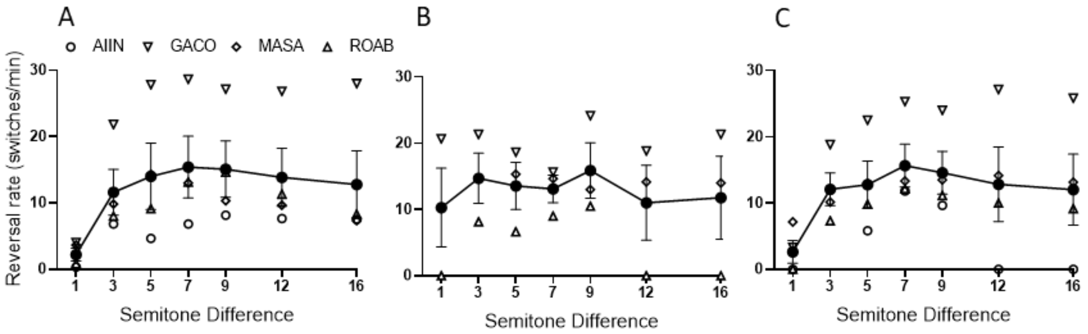

Figure 4.2. Reversal rate of each trial per each participant per each stimulus performed in the pilot. A) Results of the auditory task using the characteristics of the stimulus A. B) Results of the auditory task using the characteristics of the stimulus B. C) Results of the auditory task using the characteristics of the stimulus C.

Reversal rate was also estimated for the three stimuli which show clear differences for varying semitone differences. Increasing semitone difference appears to increase both the likelihood of perceiving the stimuli as segregated, as evident in Figure 4.1, and also the number of reversal (Figure 4.2). Reversals per minute with the stimulus A varies between 2.208 ± 1.189 reversals/min (mean ± SD) for 1 semitone difference to 12.792 ± 10.148 for 16 semitones difference, with maximum number of reversals at 7 semitones difference (15.417 ± 9.312 rev/min; Figure 3.2A). For stimulus B for the minimum and maximum semitone difference reversal rate is 10.278 ± 10.339 to 11.778 ± 10.839 rev/min, with the maximum value of reversals at 9 semitones difference (15.889 ± 7.277 rev/min; Figure 3.2B). Finally, the stimulus C resulted in 2.625 ± 3.411 to 12.042 ± 10.720 reversals per minute for the same characteristics and a maximum at 7 semitones difference (15.667 ± 6.976 rev/min; Figure 4.2C). All stimulus tested show a clear relation between ambiguity and reversal rate (semitone difference main-effect: $p < 0.0001$ for stimulus A; $p = 0.0016$ for stimulus C, two-way repeated measures ANOVA), with the exception of stimulus B (semitone difference main-effect $p = 0.0976$, two-way repeated measures ANOVA). While the number of reversals per minute shows high variability between subjects (subject main-effect: 61.5% of total variation, $p = 0.0014$ for stimulus A; 76.1% of total variation, $p = 0.0011$ for stimulus B; 52.9% of total variation, $p < 0.0001$ for stimulus C, two-way repeated measures ANOVA), it is possible to identify a tendency of reversals to decrease towards the extreme values, showing a maximum at parameters of higher ambiguity, with maximum rev/min at 7, 9 and 7 semitones for stimulus A, B and C, respectively. This is likely related to the phenomenon of increased reversal rates at equi-dominance, which has been interpreted as a result of exploratory mechanisms in the face of ambiguity (Moreno-Bote et al., 2010). Taking into account these observations and also weighing our participants own assessment of the ease with which they could perform the task and their confidence in their responses, it was decided to adopt A stimulus (Curtu et al., 2019) as our paradigm for the remainder of the psychophysical tests and the study.

4.1.2. Second pilot

In previous studies different sets of frequencies have been used to study auditory bistability, ranging from 400 to 1000Hz, so a second pilot was created to check whether performance differed between stimuli with different base frequencies. This pilot consisted of a lower pitch tone, tone B, which was the base frequency that was kept constant in each experimental condition. Three sets of frequencies for tone B were used: 400Hz, 700Hz and 1000Hz. The frequency of the B tone remained the same during all semitone differences tests, with tone A, the higher pitch tone, varying according to the differences in semitone it has relative to tone B (differences in semitones will be dependent on the base frequency relative to which it is defined, see methods section). The semitone differences used here were 2, 4, 6, 8 and 10. This pilot was performed by 3 participants, two of them researchers of the current project (GACO and MASA).

The figures 4.3 and 4.4 present the ratio of time that participants reported perceiving the sound segregated while listening to a continuous “ABA_” stimulus as a function of semitone difference between frequency A and frequency B (all other parameters set as stimulus A, see Table 4.1) and the reversal rate, per semitone difference, respectively. Each graphic shows the results for one base frequency, corresponding to the frequency of the tone B (Figure 4.3A, B and C, B_{freq} = 400, 700 and 1000Hz, respectively).

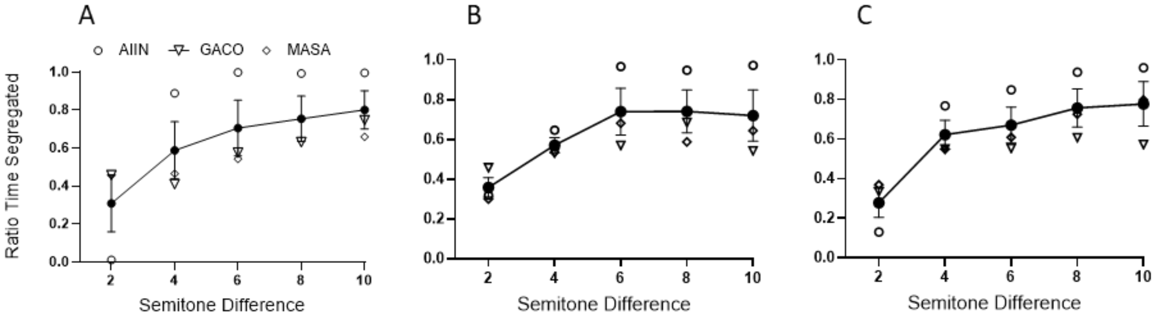

Figure 4.3 Ratio of time during the task that the observer reports perceiving the sound grouped in function of the semitone difference between frequency A and frequency B. A) Results of the auditory task using the tone B with a frequency of 400Hz. B) Results of the auditory task using the tone B with a frequency of 700Hz. C) Results of the auditory task using the tone B with a frequency of 1000Hz.

Figure 4.3 shows the relative dominance of the two percepts for the three base frequencies and a range of differences in semitones (ΔF). All three base frequencies showed the expected behaviour of increased segregated perception with an increase of semitone difference (ΔF main-effect: $p = 0.028$ for $B_{freq} = 400Hz$; $p = 0.0002$ for $B_{freq} = 700Hz$; $p < 0.0023$ for $B_{freq} = 1000Hz$, two-way repeated measures ANOVA). In all the three main base frequency conditions it was possible to find semitone differences that favour grouped perceptions (ratio < 0.5) and semitone differences that favour segregated perception (ratio > 0.5). For the stimulus with tone B of 400Hz the relative segregated perception varies from 0.308 ± 0.256 for a semitone difference of 2 to 0.8 ± 0.175 for a semitone difference of 10 (Figure 4.3A). For a tone B of 700Hz the relative segregated perception varies between 0.359 ± 0.088 to 0.726 ± 0.225, for 2 and 10 semitones difference (Figure 4.3B), respectively. Finally, for 1000Hz of base tone, the relative dominance is 0.278 ± 0.129 for 2 semitones and 0.777 ± 0.195 for 10 semitones difference (Figure 4.3C). As our study intend to explore the range of conditions which could produce a dominant perception of either of the percepts, the three stimuli appear suitable for, as varying the parameter ΔF resulted in grouped dominant stimuli (ratio < 0.5) and segregated dominant stimuli (ratio > 0.5) for all B_{freq} conditions.

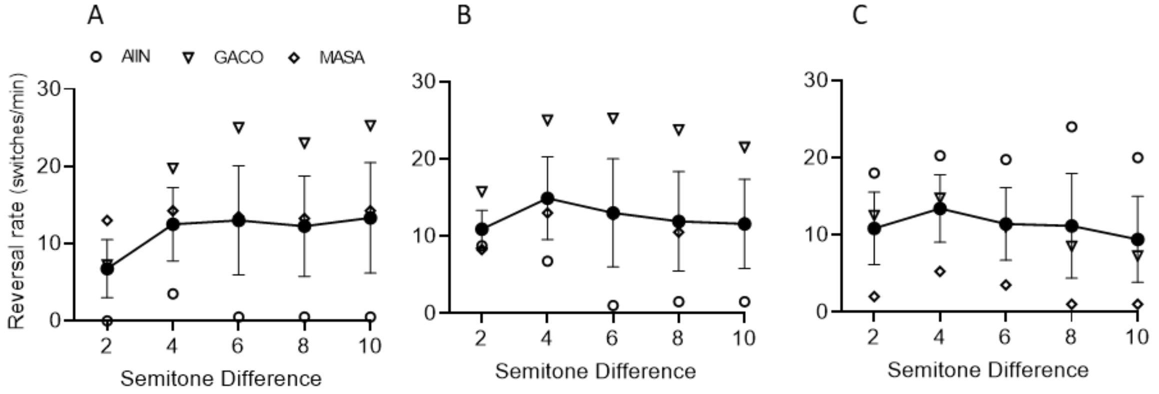

Figure 4.4 Reversal rate per each subject per semitone difference. A) Results of the auditory task using the tone B with a frequency of 400Hz. B) Results of the auditory task using the tone B with a frequency of 700Hz. C) Results of the auditory task using the tone B with a frequency of 1000Hz.

Analysing the reversal rates for the three B_{freq} stimuli, increasing semitone difference does not lead to significantly different reversal rates ($p > 0.05$, ns, two-way repeated measures ANOVA). This is probably due to the limited range of semitones tested (2-10 instead of 1-16 semitones tested in the first pilot; see Figure 4.2). In the first stimulus the reversal rate ranges from 6.75 ± 6.514 (rev/min) for 2 semitones to 13.333 ± 12.4 (rev/min) when tone A and B had 10 semitones of difference. When B_{freq} equals 700Hz, the reversals per min range from 10.917 ± 4.193 (rev/min), 2 semitones, to 14.917 ± 9.275 (rev/min) for 4 semitone difference. In the last stimulus used in the second pilot of the auditory ambiguous stimulus, the minimum value of the reversal rate was at 10semitones difference with 9.417 ± 9.689 (rev/min) and the maximum value was of 13.413 ± 7.588 (rev/min) when the semitone difference was 4 semitones. No significant differences were found in the reversal rate with the increasing of the semitone difference (ΔF main-effect: $p = 0.2304$ for $B_{freq} = 400Hz$; $p = 0.3152$ for $B_{freq} = 700Hz$; $p = 0.4254$ for $B_{freq} = 1000Hz$, two-way repeated measures ANOVA). However, a significative difference between subjects was found, similarly to the first pilot (subject main-effect: $p = 0.0444$ for $B_{freq} = 400Hz$; $p = 0.0024$ for $B_{freq} = 700Hz$; $p = 0.0046$ for $B_{freq} = 1000Hz$, two-way repeated measures ANOVA). All three conditions resulted in similar reversal rates on average over all semitone differences testes: 11.57 ± 2.73, 12.47 ± 1.56 and 11.25 ± 1.44 rev/min for B_{freq} of 400Hz, 700Hz and 1000Hz respectively ($p = 0.86$, ns, one-way ANOVA).

Tone B with frequency of 1000Hz resulted in the lowest value of the ratio for segregated perception, that is a higher dominance of grouped perception, and the widest range of ratios in the tested conditions. Also, because B_{freq} of 1000Hz is the most common used, it was decided to maintain this characteristic in the rest of the experiment (Gutschalk et al., 2005, Sanders et al., 2018, Curtu et al., 2019).

Finally, it was tested whether tone order, ie. high tone-low tone- high tone, the ABA_ order, or low tone-high tone-low tone, BAB_, affected performance but no apparent differences were found (data not shown). Hence, the first configuration, ABA_, was maintained as it is the most commonly used in bistable auditory paradigms (Gutschalk et al., 2005, Billig et al., 2018, Curtu et al., 2019).

4.2. Individual calibration of bistability

In this sub-section we show the results and discussion of the calibration methods utilized in the current experiment for both visual and auditory tasks, as well as estimated parameters for each stimulus to be employed in the EEG study of biased bistable perception.

4.2.1. Visual task

The Method of Constant Stimuli, resulted in a series of vertical motion percept dominance percentages, one for each aspect ratio tested by each participant. The tested aspect ratios were selected based on each individuals' PR previously determined by the MoL (see section 3.4.1). Table 4.2 shows the results from MoCS for each participant.

Table 4.2. Values of dominance of the vertical motion perception for each participant for each aspect ratio used in visual stimulus.

Subject	1º Ratio	2º Ratio	3º Ratio	4º Ratio	5º Ratio	6º Ratio	7º Ratio	8º Ratio
BEAR	0.358	0.438	0.516	0.598	0.504	0.679	0.766	0.868
BRSA	0.400	0.381	0.480	0.561	0.574	0.644	0.742	0.760
DAAG	0.195	0.361	0.534	0.600	0.627	0.620	0.789	1.000
FIAM	0.292	0.325	0.561	0.651	0.642	0.609	0.724	0.917
GACO	0.275	0.306	0.419	0.526	0.574	0.652	0.820	0.920
JOPA	0.267	0.400	0.533	0.564	0.507	0.591	0.843	0.828
JUSO	0.154	0.388	0.383	0.584	0.393	0.583	0.892	0.895
MAPA	0.222	0.393	0.468	0.584	0.470	0.624	0.884	0.931
MASA	0.094	0.317	0.395	0.515	0.643	0.652	1.000	1.000
PECA	0.171	0.141	0.475	0.594	0.389	0.919	0.888	0.945
SAMO	0.212	0.311	0.341	0.413	0.630	0.870	0.866	0.925
SANE	0.156	0.000	0.513	0.500	0.941	0.549	1.000	1.000

With these results, the psychometric fits were estimated using a Logistic function (Palamedes toolbox, Prins and Kingdom, 2018). The parameters used for Υ, corresponding to the guessing rate, and λ, lapse rate, were both set to 0. From the individual fits, the values of 35% and 65% vertical perception were obtained for each participant. Figure 3.5 shows the psychometric curves of the visual stimulus for all subjects.

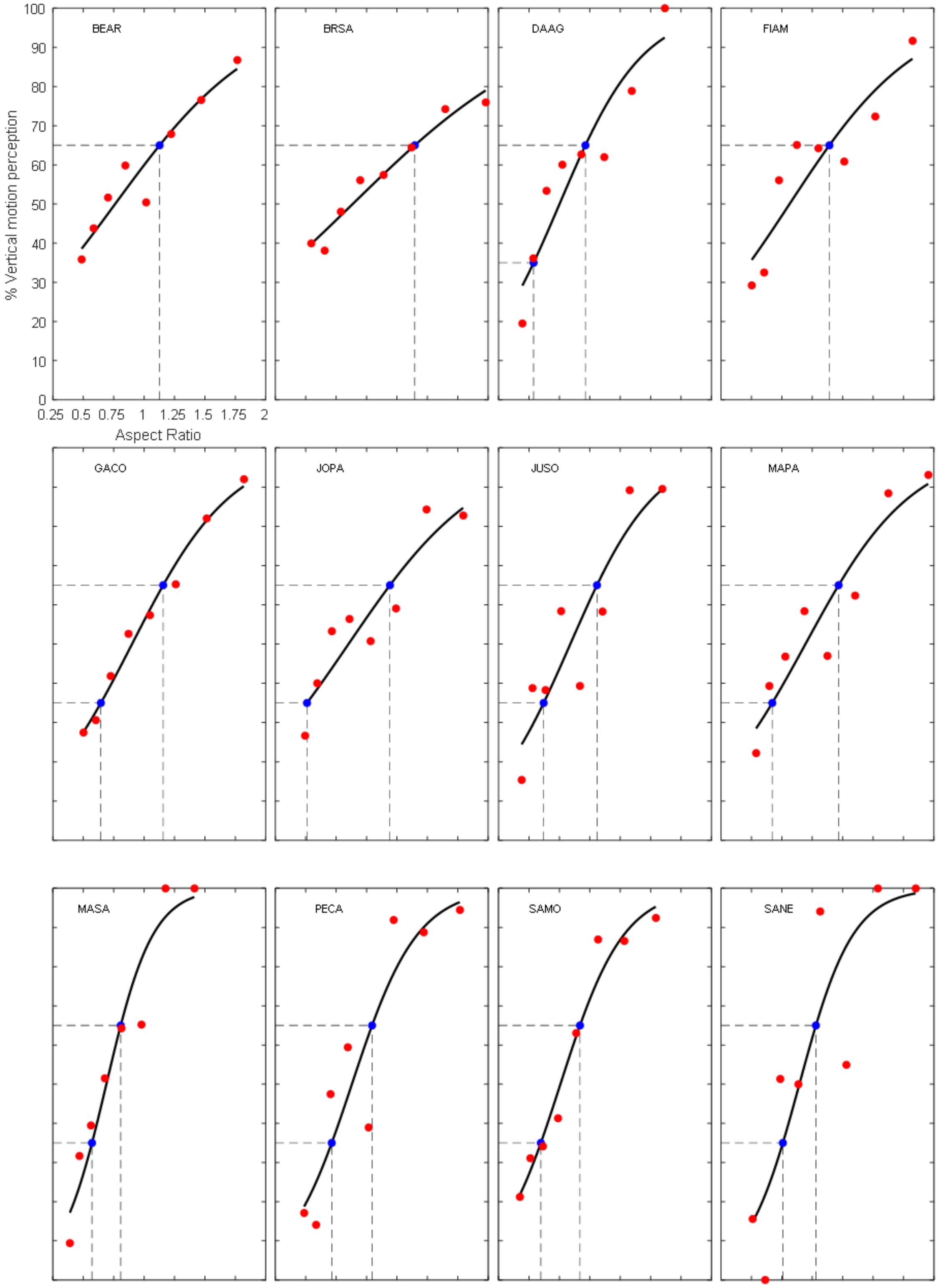

Figure 4.5. Psychometric curves from the behaviour of the subjects during the visual stimulus. The graphic represents the dominance of the vertical motion perception in relation of aspect ratio. The red dots are the 8 ratios used during MoCS and the blue dots are the points of 35% and 65% dominance of vertical motion perception, respectively

While the range of tested conditions was sufficient to adequately fit the majority of participants, the point of 35% dominance of vertical motion perception was beyond the lowest tested ratio for three subjects (BEAR, BRSA and FIAM). It was decided to advance with all the twelve subjects for the EEG part of the procedure, using for these subjects the lowest ratio tested in the MoCS, in the EEG experiment (described in detail further). All the curves have a p-value of the deviance higher than 0.05 obtained by using a Goodness-of-fit that was estimated using resampling and Monte Carlo simulations (see Methods, Wichmann and Hill, 2001, Kingdom and Prins, 2010).

4.2.2. Auditory task

As with the visual stimuli, MoCS results of segregated percept dominance percentages for each semitone difference tested were obtained. In the auditory task it is intended to bias the perception of the participants towards either of the two percepts in each experimental setting. For that, it is necessary to construct psychometric curves to find the values of semitone difference that results in specific percentages of time viewing segregated percept. As with the visual study, it was considered to use the MoL followed by MoCS to obtain individual psychometric functions, but the gradual increase or decrease in the semitone difference resulted in fairly robust adaptation making participants change perception much earlier than what would eventually be determined to be their 50% threshold. Moreover, the semitone difference needed for the segregated percept to be consistently heard by the subjects was too high, exacerbating the adaptation effect and increasing the error in estimation of the threshold. Hence, it was decided not to use the combination MoL and MoCS to plot the curve and it was just used MoCS with the same predefined semitone difference for all the participants in the study. It was latter observed that, contrary to the visual stimulus, SAM, the bistable auditory stimulus, ABA, did not vary as much between subjects, making it adequate to use the same 8 conditions to adjust a psychometric function for most subjects.

In table 4.3 the results from MoCS are presented for each subject.

Table 4.3. Values of dominance of the segregated perception for each participant for each semitone difference used in the auditory stimulus.

Subject	**1**	**2**	**3**	**6**	**9**	**12**	**16**	**22**
BEAR	0.103	0.297	0.347	0.473	0.738	0.698	0.815	0.949
BRSA	0.089	0.188	0.279	0.382	0.658	0.665	0.575	0.579
DAAG	0.000	0.151	0.304	0.263	0.678	0.628	0.712	0.796
FIAM	0.662	0.624	0.596	0.647	0.638	0.685	0.637	0.677
GACO	0.231	0.346	0.414	0.360	0.507	0.493	0.724	0.757
JOPA	0.021	0.231	0.474	0.668	0.774	0.764	0.950	0.990
JUSO	0.000	0.029	0.494	0.822	0.809	0.884	0.916	0.797
MAPA	0.000	0.111	0.296	0.572	0.683	0.843	0.981	0.950
MASA	0.173	0.277	0.403	0.426	0.621	0.728	0.789	0.933
PECA	0.000	0.203	0.378	0.458	0.408	0.560	0.609	0.793
SAMO	0.000	0.153	0.280	0.310	0.451	0.403	0.513	0.715
SANE	0.071	0.249	0.560	0.608	0.634	0.630	0.820	0.923

The relative dominance of each percept was fitted to a psychometric function using a Weibull function and the Palamedes toolbox (Prins and Kingdom, 2018). The parameters for guessing (γ) and lapse rates (λ) used were also both set to zero, as in the SAM task. The Weibull function was chosen due to the psychometric functions for auditory bistability being best described by a Weibull distribution with a "shape" parameter (β) between 0 and 1 ($\beta < 1$), i.e. a curve that asymptotes to 100% in a linear abscissa (May and Solomon, 2013). Figure 4.6 presents the psychometric curves obtained for the auditory stimulus for all the participants. The points of 35% and 65% of segregated perception dominance were calculated and plotted alongside the psychometric curves (blue dots). Figure 4.6 shows the psychometric curves of the auditory stimulus for all subjects.

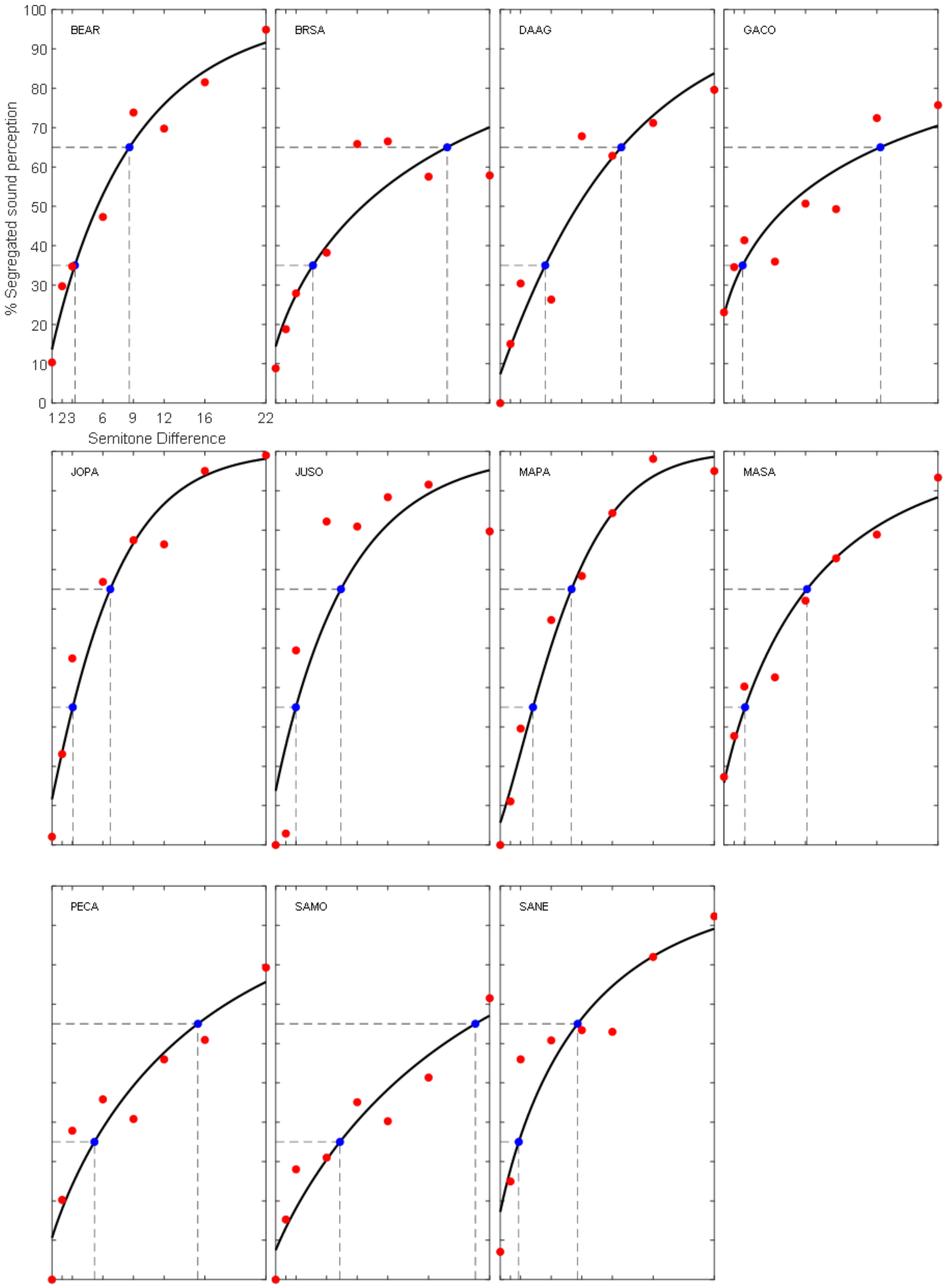

Figure 4.6. Psychometric curves from the behaviour of the subjects during the auditory stimulus. The graphic represents the dominance of the segregated sound perception in relation of semitone difference. The red dots are the 8 ratios used during MoCS and the blue dots are the points of 35% and 65% dominance of segregated sound perception, respectively.

The curve of the subject FIAM is not represented as this subject displayed a relative dominance of the segregated perception between 55% and 69% in all conditions tested, hence all were above 50% segregated perception even with the largest difference of 22 semitones. For this reason, the calibration was considered inadequate and the subject was excluded from the EEG part of the experiment. All the subjects showed good psychometric curves as it was possible to fit reasonably their data. All the curves have a p-value of the deviance higher than 0.05 using a Goodness-of-fit estimate using resampling and Monte Carlo simulations (see Methods, (Wichmann and Hill, 2001, Kingdom and Prins, 2010))

It is possible to conclude as well the majority of subjects we were able to achieve stimuli favouring either of the two perceptions that the Auditory Streaming provides (Noorden, 1975).

4.2.3. Estimated parameters for biased perception

As previously said, from the psychometric curves obtained from the calibration it was possible to obtain the values of aspect ratio/semitone difference for the experimental conditions of biased perception in the EEG experiment. Aspect ratios and semitone difference for the SAM and the ABA stimuli to be used in the EEG experiment are shown in Table 4.4.

Table 4.4. Values of ratio and semitone difference used in the psychophysical tasks performed during the EEG acquisition.

Subject	35% Vertical Perception SAM	65% Vertical Perception SAM	35% Segregated Perception ABA	65% Segregated Perception ABA
BEAR	0.49	1.13	3.25	8.60
BRSA	0.55	1.40	4.66	17.82
DAAG	0.54	0.96	5.41	12.88
FIAM	0.50	1.14	-	-
GACO	0.64	1.16	2.83	16.35
JOPA	0.51	1.19	3.04	6.72
JUSO	0.62	1.06	2.98	7.41
MAPA	0.65	1.22	4.22	8.00
MASA	0.57	0.81	3.07	9.14
PECA	0.71	1.05	5.17	15.32
SAMO	0.60	0.92	7.31	20.59
SANE	0.76	1.03	2.82	8.60

The values that are shaded grey correspond to the ones extracted from the psychometric fit falling outside the sampled área.

4.3. EEG

In this sub-section, the results from the EEG experiment are presented and discussed.

First an analysis of the behavioural data of both perceptual tasks was performed to assess individual performance and whether the selected conditions produced a bistable state with a biased dominance as intended.

4.3.1. Behavioural Analysis

During the EEG recording, subjects performed several runs of each perceptual task, consisting of a continuous presentation of each bistable stimulus, in which they were instructed to continuously report their current perception. Tasks for both the visual paradigm, SAM, and the auditory, BAU, required button presses for reporting vertical or horizontal movement, in the former, and grouped or segregated perception, in the latter.

The dynamics of perceptual bistability for both conditions of biased visual perception were analysed based on perceptual dominance of each percept (Figure 4.7). SAM stimuli with aspect ratios (width/height) defined based on individual calibrations (Table 4.4) were utilized in order to skew perception toward a horizontal motion, mean aspect ratio of 0.58 ± 0.08 (mean ± SEM; Figure 4.7A), and towards a horizontal motion, mean aspect ratio of 1.10 ± 0.15 (mean ± SEM; Figure 4.7B). These ratios were selected in order to produce biased SAM stimuli with a probability of being perceived describing vertical motion 35% of the time (horizontally biased) or 65% of the time (vertically biased).

The figure 4.7 presents the results of the visual psychophysical task during the EEG acquisition.

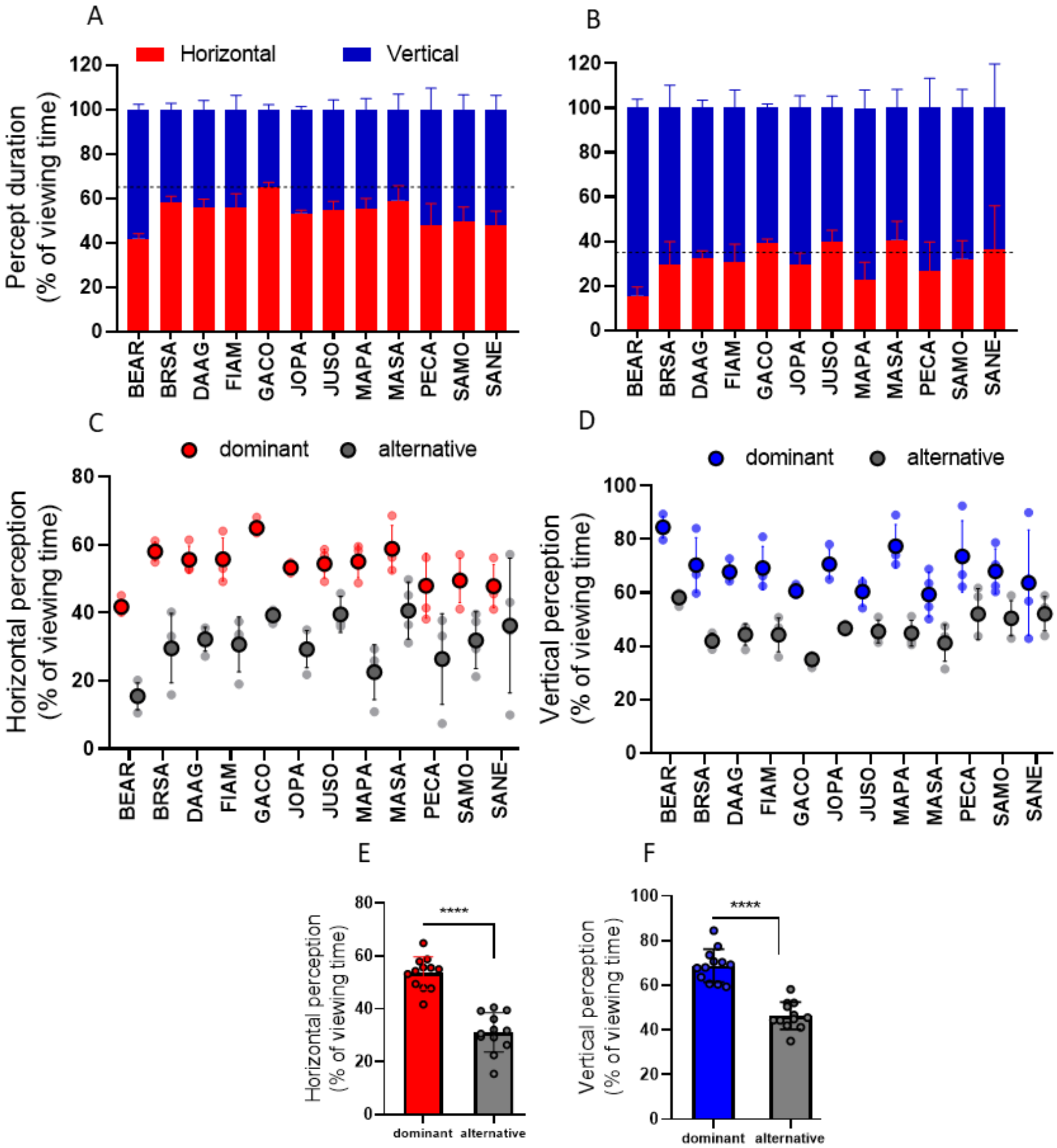

Figure 4.7 Psychophysical results of the visual task. The graphics A and B represent the percentage of viewing time of each percept in the runs with the lowest aspect ratio (A) and in the runs with the highest aspect ratio(B), per each subject. The graphic C represents the percentage of viewing time of horizontal motion perception per each subject when this perception is dominant and when it is the alternative one. The graphic D represents the percentage of viewing time of vertical motion perception per each subject when this perception is dominant and when it is the alternative one. The graphic E represents the average of the percentages of viewing time of horizontal perception of all subject, separated by the ones that were during runs with lowest aspect ratio (dominant perception) and the ones during runs with highest aspect ratio (alternative perception). The graphic F represents the average of the percentages of viewing time of vertical perception of all subject, separated by the ones that were during runs with lowest aspect ratio (alternative perception) and the ones during runs with highest aspect ratio (dominant perception). **** $p < 0.0001$.

Perception of horizontal motion was higher relative to vertical motion for SAM with smaller aspect ratio ($p < 0.05$, one-tailed t-test; Figure 4.7A), with an average percentage of time viewing the dots moving horizontally of 53.60 ± 6.10% (mean ±SD). This condition was expected to result in a dominance of horizontal motion perception, with around 65% of viewing time corresponding to horizontal motion, while 35% would account for vertical motion. While the majority of participants displayed the expected horizontal dominance, four subjects showed a total time of perceiving horizontal motion below 50% (41.77 ± 2.29, 48.00 ± 9.53, 49.52 ± 6.58, 47.86 ± 6.37 % of horizontal perception, mean ± SD, for BEAR, PECA, SAMO and SANE, respectively), indicating that either the calibration protocol was not successful for these subjects or that these show higher variability between different test runs. Nonetheless, the majority of subjects did perceive horizontal motion for more than half of the time, meaning it was possible to bias SAM, a stimulus typically biased towards vertical perception (Genc et al., 2011), towards horizontal perception.

The opposite effect was observed when viewing SAM with a higher aspect ratio: a dominant perception of vertical motion is evident (vertical perception > 50%, $p < 0.0001$, one-tailed *t*-test), with 68.93 ± 7.41% (mean ± SD) of the time accounting for vertical perception (Figure 4.7B). Under this condition all subjects displayed a bias towards vertical perception, with a minimum of 59.36 ± 8.39% of viewing time (Figure 4.7D). The expected effect of biasing the vertical percept towards 65% of the viewing time was achieved taking into account all subjects (mean dominance vs 65%, $p = 0.1$, ns, two-tailed *t*-test). While such a precise result was not achieved with the horizontally biased SAM (53.60 ± 6.10% average Horizontal dominance < 65%, p < 0.0001, two-tailed *t*-test), a comparison of the time perceiving horizontal motion for the horizontally dominant SAM (low width/height ratio) and for the vertically dominant SAM (high width/height ratio), reveals that for the former SAM configuration horizontal perception is more dominant than for the latter configuration (Figure 4.7C and E). This difference between duration of horizontal perception for the horizontally biased SAM and the vertically biased SAM are highly significant ($p << 0.0001$, two-tailed *t*-test; Figure 4.7E) and thus the same horizontal percept can be defined as “dominant” in the former configuration of SAM and as “alternative” in the latter.

This is also the case for the vertical percept, being more dominant in the vertically biased SAM and being closer to an alternative in the horizontally biased SAM ($p << 0.0001$, two-tailed *t*-test; Figure 4.7F). These results show that the SAM visual stimulus, while maintaining its ambiguity, was successfully biased towards either of the two percepts.

The figure 4.8 presents the results of the auditory psychophysical task during the EEG acquisition.

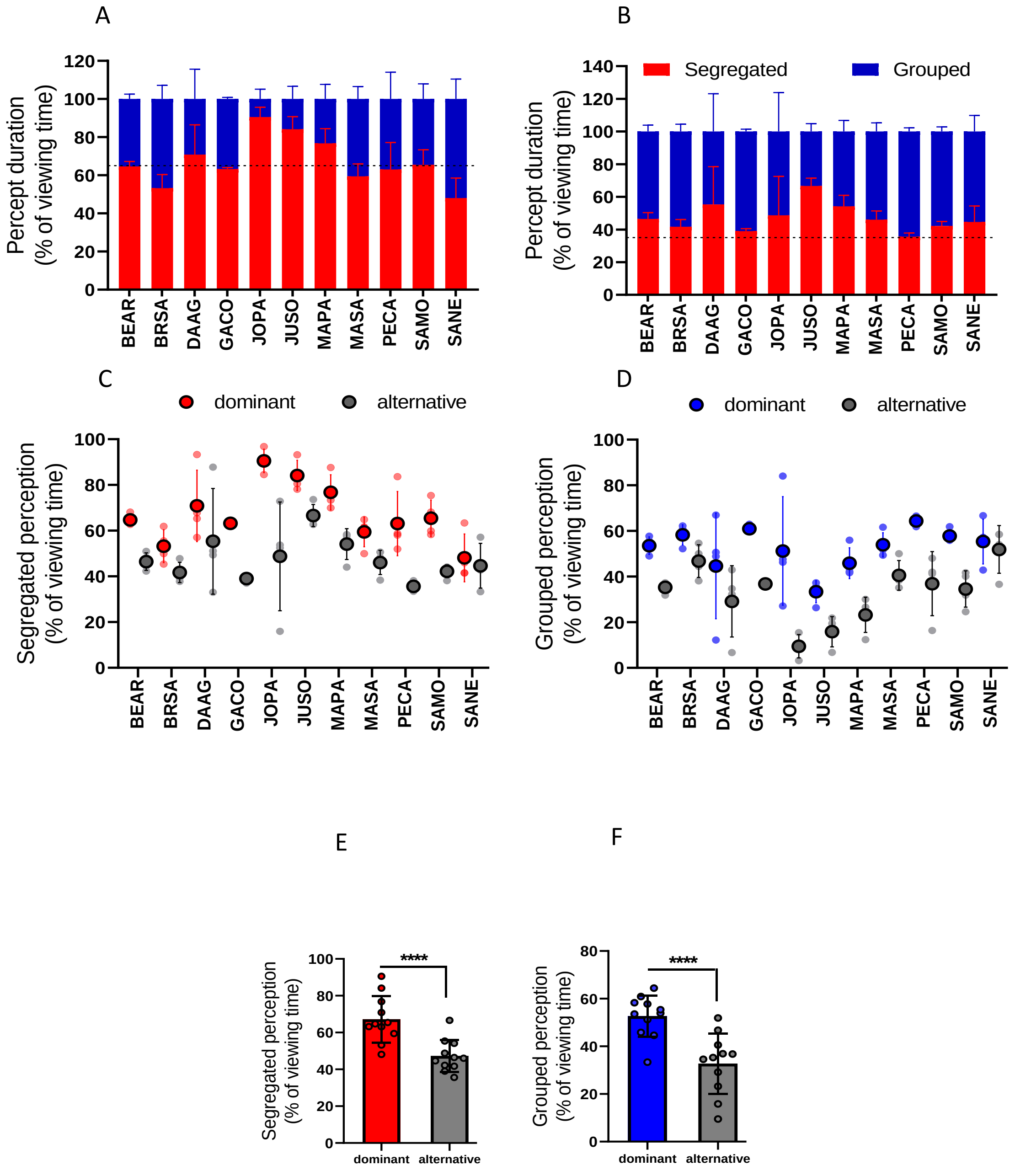

Figure 4.8 Psychophysical results of the auditory task. The graphics A and B represent the percentage of viewing time of each percept in the runs with the lowest semitone difference (A) and in the runs with the highest semitone difference(B), per each subject. The graphic C represents the percentage of viewing time of segregated perception per each subject when this perception is dominant and when it is the alternative one. The graphic D represents the percentage of viewing time of grouped perception per each subject when this perception is dominant and when it is the alternative one. The graphic E represents the average of the percentages of viewing time of segregated perception of all subject, separated by the ones that were during runs with lowest semitone difference (alternative perception) and the ones during runs with highest semitone difference (dominant perception). The graphic F represents the average of the percentages of viewing time of grouped perception of all subject, separated by the ones that were during runs with highest semitone difference (alternative perception) and the ones during runs with lowest semitone difference (dominant perception). **** $p < 0.0001$.

The same approach was employed for analysing the auditory bistable stimuli biased towards either grouped or segregated percepts (Figure 4.8). As with the influence of horizontal and vertical distances over the dominance of horizontal or vertical motion in SAM, the distance between tone frequencies influences perception in a similar way. For the ABA_ stimulus with the smallest ΔF between tones (average ΔF = 4.1 semitones, individually determined, see table 4.4), grouped perception corresponded to 52.67 ± 8.70% of viewing time, versus 47.33 ± 8.70% for segregated perception ($p = 0.17$, ns, one-tailed *t*-test; Figure 4.8A). It was expected that under these conditions, the grouped percept of the sound should be the dominant with 65% of the viewing time. More importantly, grouped perception should be decidedly dominant (> 50% of viewing time), a condition which was not met for three out of the 12 subjects (44.66 ± 23.15, 33.38 ± 4.84 and 45.86 ± 6.78% of grouped perception, mean ± SD, for DAAG, JUSO and MAPA , respectively). The reasons for this outcome have been discussed previously (section 4.3.1) but also adaptation might play a predominant role in the auditory paradigm (Rankin et al., 2017).

On other hand, for the high semitone difference condition the intended dominant percept of segregated perception was in fact the most likely to be perceived, as the larger semitone difference separating the frequencies of tones A and B resulted in increased segregated perception (Figure 4.8B). Only one subject (SANE) did not perceive this segregated configuration as dominant (48.09 ± 10.43% of segregated perception, mean ± SD), while the percentage for the remaining 10 subjects did result in an above 50% dominance for the segregated percept. The mean segregated perception for all subjects was 67.22 ± 12.65% of viewing time (not significantly different from the intended 65%, $p = 0.57$, ns, two-tailed *t*-test). Once again, one of the biased conditions, segregated biased ABA, resulted in a closer approximation of the intended effect than the other, namely the grouped biased ABA (52.67 ± 8.70% of perceived time, significantly different from 65%, $p < 0.0008$, one-sample t-test).

A comparison of perceptual dominance of grouped and segregated percepts still shows that each percept was much more prevalent for the ABA stimuli intended to bias towards that percept (Figure 4.8C and D). A clear effect for all subjects to perceive segregated streams when listening to the segregated biased ABA (Figure 4.8C, dominant condition) compared to the same perception when listening the grouped-biased ABA (Figure 4.8C, alternative condition). Note that in these graphs the runs where one perception should be dominant are separated from the ones that the same perception should be alternative. The same effect is observed for the grouped perception over grouped-biased and segregated-biased ABA (Figure 4.8D, dominant and alternative, respectively). One can thus conclude that, despite smaller differences in some subjects (e.g. SANE), a percept was always more prevalent in a ABA stimuli where the percept should be dominant than in the ABA stimuli where it should be an alternative percept (dominant vs alternative $p << 0.0001$, two-tailed *t*-test; Figure 4.8E and F).

4.3.2. Selection of volunteers and datasets for analysis

Based on the behavioural results obtained in tandem with the EEG recording, and taking into account the expected performance, it was decided that either certain runs or certain subjects did not meet the criteria to be included in further analysis. The first criteria required that on average the intended dominant perception for that particular experiment should represent more than 50% of the viewing time for at least two of the four runs. If for instance, in four runs that the vertical motion perception it is supposed to be dominant, its percentage of time reported is less than 50% in three of those runs, all the data from this subject is excluded for the SAM experiment. This was a necessary condition to be met since otherwise it would indicate an inadequate calibration and the inclusion of data that does not adhere to the desired experimental set up, that is having a dominant and an alternative percept in bistable perception. Using this criterion, the following data was excluded:

- The visual task from the subject BEAR;
- The visual task from the subject SANE;
- The auditory task from the subject JOPA;
- The auditory task from the subject JUSO;
- The auditory task from the subject MAPA;
- The auditory task from the subject SANE;

After the removal of the subjects that did not show the expected performance in the bistable tasks, perception of horizontal motion during horizontal-biased SAM was on average 55.35 ± 4.78% of viewing time (mean ± SD; > 50%, $p = 0.0032$, one-sampled one-tailed *t*-test) and vertical motion during vertically biased SAM was 67.77 ± 5.97% (> 50%,

$p < 0.0001$)For the auditory stimuli, segregated perception during segregated-biased ABA was 62.85 ± 5.46% (> 50%, $p = 0.0004$) and grouped perception during grouped-biased ABA was 56.22 ± 6.35% (> 50%, $p = 0.02$).

The second criteria was that, in case a subject displayed a maximum of two runs that did not adhere to the expected performance, i.e. the dominant percept did not get reported more than 50% of the time, these specific runs were excluded from analysis. The following runs were excluded from analysis: Also, a run with 100% dominance of the supposed dominant perception was excluded.

- BEAR: one run in the auditory task with low semitone difference;
- BRSA: two runs in the auditory task, both with high semitone difference;
- DAAG: two runs in the auditory task, both with low semitone difference;
- FIAM: one run in the visual task with low aspect ratio;
- JUSO: two runs in the visual task, one with low aspect ratio and another with high aspect ratio;
- MAPA: one run in the visual task with low aspect ratio
- MASA: two runs in the auditory task, one with low semitone difference and another with high semitone difference;
- PECA: two runs in the visual task, both with low aspect ratio;
- SAMO: two runs in the visual task, both with low aspect ratio.

With the elimination of these runs the perception of horizontal motion during horizontal-biased SAM was on average 57.21 ± 3.25% (mean ± SD; > 50%, $p < 0.0001$) and the perception of vertical motion during vertical-biased SAM was on average 67.77 ± 5.97% (> 50%, $p < 0.0001$). In the auditory stimulus data, the removal of some considered as ‘bad’ runs changed the average of perceiving the sound as grouped during grouped-biased ABA to 58.67 ± 3.22% (> 50%, $p = 0.0002$) and the average of perceiving segregated streams of sound during segregated-biased ABA turned to 64.09 ± 3.66% (> 50%, $p < 0.0001$).

These psychophysical results show that the method calibration of the auditory stimulus have some flaws that must be corrected. This is due to the lack of research in this field. Although a lot of this ambiguity is known (Pressnitzer and Hupe, 2006, Billig et al., 2018, Curtu et al., 2019), research around the value of semitone difference in which a subject perceives 50% of the time segregated sound and 50% of the time groups sound is still missing. So, the method used in this study to find specific semitone difference correspondent to certain dominances might not be rigorous enough.

It is normal that the value of semitone difference that makes the observer report for 50% of the time one perception is different for each person. The method of Constant Stimuli was applied, but the semitone differences used were the same for every observer, in contrast to what happened during the calibration of the visual stimulus. The reason that in two subjects the calibration method performed for the visual stimulus did not work as expected it is still unclear, the method was applied in the same way for every participant. However, this is a not exact method and is highly dependent of the user, their attention and concentration during both phases of the experiment.

After the removal of the data not suited to the experiment, it was followed to the pre-processing and analysis of the EEG data with 10 subjects of the visual task and 7 subjects of the auditory task.

4.4. Oscillations related to perceptual changes

From the EEG recordings during each perceptual task, i.e. SAM for visual bistability and ABA for auditory bistability, the beta activity preceding and following a report of perceptual change was estimated. Several studies have identified beta activity associated with bistability and the perception of alternative configurations of ambiguous stimuli (VanRullen et al., 2006, Piantoni et al., 2010, Zaretskaya and Bartels, 2015). Here we intend to identify spectral changes related to perceptual changes and, moreover, differences in beta activity that signal distinct percepts of both visual, SAM, and auditory, ABA_, stimuli. The spectrograms and the curves representing the absolute power of beta band oscillations for all the selected data (see section 4.3.4) described and discussed below.

4.4.1. Beta activity during SAM perceptual changes

The figure 4.9 represents the results for the ambiguous visual task.

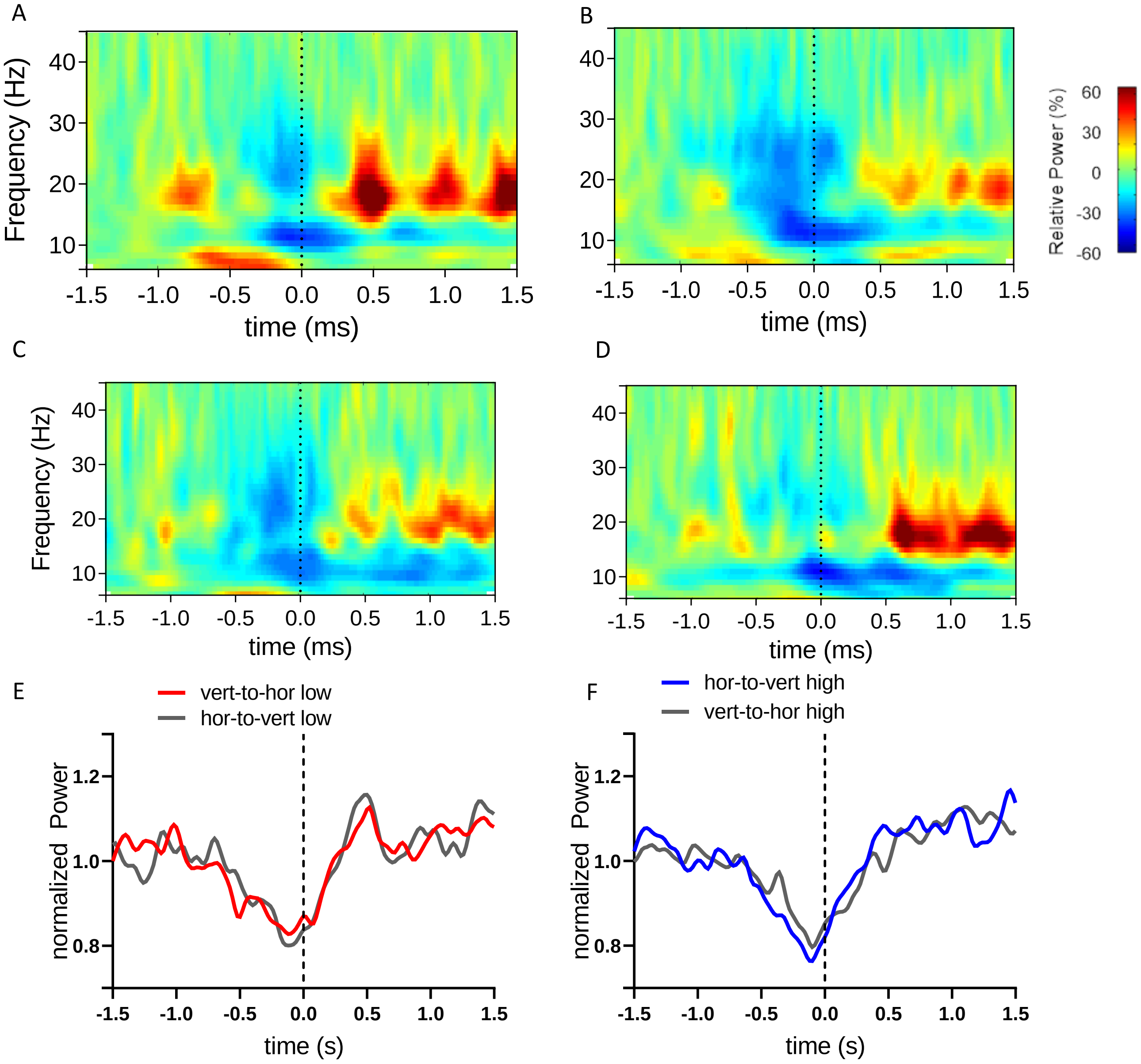

Figure 4.9 Results of the time frequency analysis in for the ambiguous visual task. Images A, B, C and D represent spectrograms and the moment zero seconds represent the moment in which the observer reports a change. Time-frequency plots of transitions horizontal to vertical (A) and vertical to horizontal (C) when the aspect ratio is low (horizontal motion perception is the dominant and vertical motion is the alternative). Time-frequency plots of transitions horizontal to vertical (B) and vertical to horizontal (D) when the aspect ratio is high (vertical motion perception is the alternative). Baseline for all time-frequency plots is -1.5 sec to -1.0 sec. E) Time course of the beta band normalized power during perceptual changes in the horizontally biased SAM. Red represents the transition from the alternative perception to the dominant and grey represents the opposite reversal. F) Time course of the beta band normalized power during perceptual changes in the vertically biased SAM. Blue represents the transition from the alternative perception to the dominant and grey represents the opposite reversal.

Epochs of perceptual change towards either vertical perception (Figure 4.9A and B) or horizontal perception (Figure 4.9C and D) were defined from the two stimulus conditions of SAM tested: one of low aspect ratio referred to as horizontally biased SAM (Figure 4.9A,C and E); and another of high aspect ratio referred to as vertically biased SAM

(Figure 4.9B, D and F). The oscillatory activity was estimated and averaged for all channels, resulting in a single time-frequency plot for each perceptual change. This approach was used to avoid an extensive search over channel/sensor-space since beta activity (13 – 30 Hz) in ambiguous paradigms have been found distributed over dispersed areas (VanRullen et al., 2006, Piantoni et al., 2010), but mainly since this method was effective in identifying beta activity in a variety of such paradigms (VanRullen et al., 2006, Piantoni et al., 2010, Aissani et al., 2014, Zaretskaya and Bartels, 2015). As can be observed in the Figure 4.9A and C, around 0.5s before the subject to report the reversal there is a decrease in power of beta band oscillations in both situations, when the perception changes from the dominant (horizontal) to the alternative percept (vertical) and when the perception changes from the alternative to the dominant percept. This decrease in beta activity in the moment of the reversal is a well-known phenomenon, frequently replicated and might be caused by the motor response that is needed to report the perceptual change but has also been interpreted as activity signalling a change in the current brain state, the perceptual *status quo* (Engel and Fries, 2010).

After the reversal there is an increase in beta activity from 250msec till 1500msec after the report of the reversal, when power stabilizes, once again, for both situations of alternation. In the current paradigm of biased visual perception, we expect to find increased beta activity for a perceptual change to a dominant perception, as previously proposed by Piantoni et al (2010). For a horizontally biased SAM (Figure 4.9A, C and E) this would result in an increase in beta activity after changing to a horizontal percept. This effect is not clear from the spectrograms, in fact the opposite seems to be the case, an increase in beta when perception changes to the alternative vertical percept. Nonetheless, this difference in beta is not significantly different between the two perceptual reversals (Figure 4.9E; $p > 0.05$, nonparametric cluster-based statistic using the Monte Carlo permutations) and the strong beta band increase observed in Figure 4.9A after the reversal but might be caused by the baseline that was applied for visualization purposes using the interval from -1.5s to -1s.

The same observation holds true for the oscillatory activity measured during perceptual changes towards the vertical dominant percept and the horizontal alternative percept (Figure 4.9B, D). From a cursory view of the spectrogram it might appear that beta is increased post-change to horizontal, but no differences were found in the time course of beta power (Figure 4.9F; $p > 0.05$, nonparametric cluster-based statistic).

4.4.2. Beta activity during SAM real change

The figure 4.10 represents the results for the unambiguous visual task.

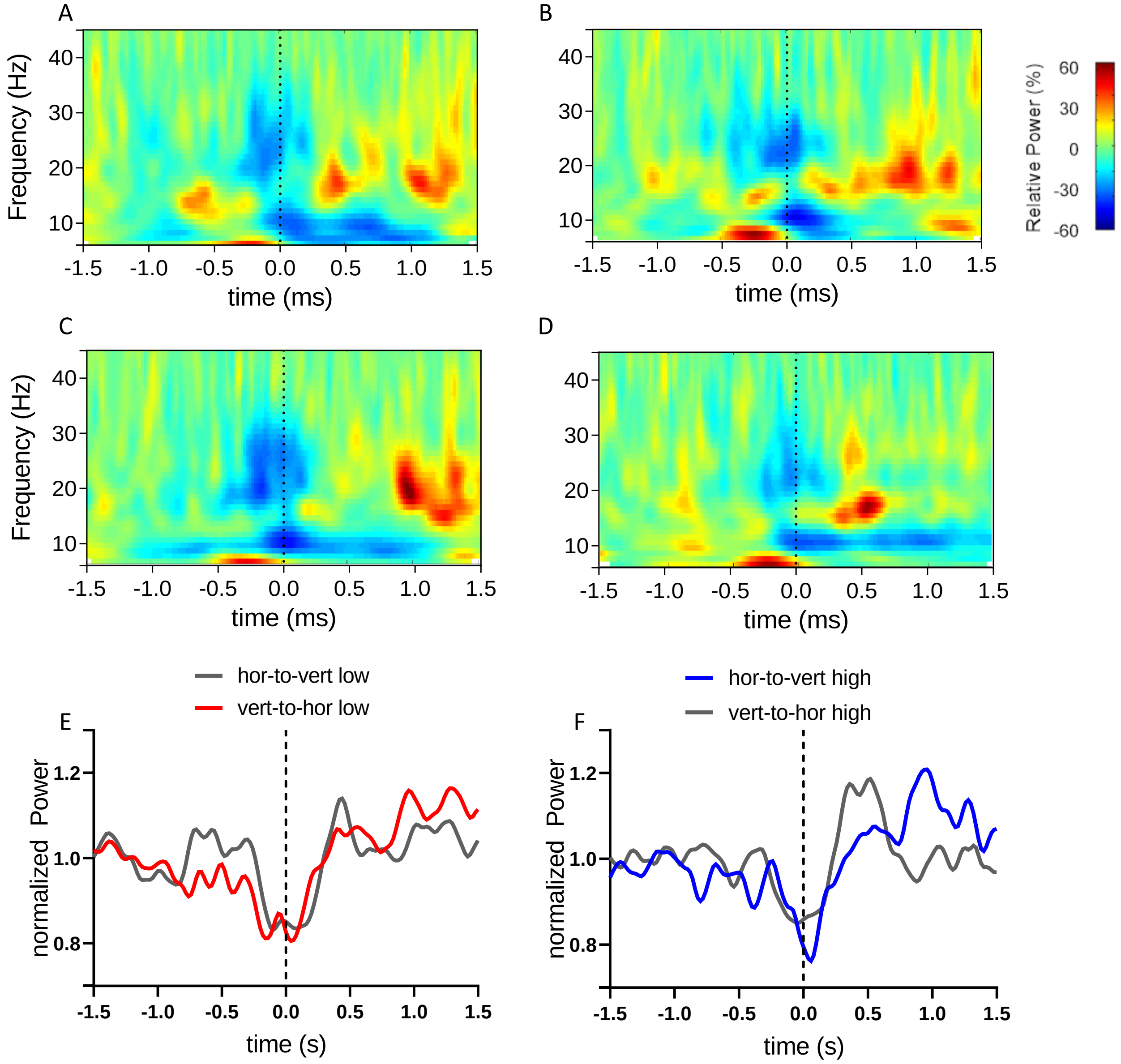

Figure 4.10 Results of the time frequency analysis in for the unambiguous visual task. Spectograms and beta power time course around the moment of reported real change. A) Time-frequency plot of transitions from horizontal to vertical when the behaviour was mimicked from runs with the low aspect ratio (vertical motion perception is the alternative). B) Spectogram of transitions horizontal to vertical when the behaviour was mimicked from runs with the high aspect ratio (vertical motion perception is the dominant). C) Spectogram of transitions vertical to horizontal when the behaviour was mimicked from runs with the low aspect ratio (horizontal motion perception is the dominant). D) Spectogram of transitions vertical to horizontal when the behaviour was mimicked from runs with the high aspect ratio (vertical motion perception is the alternative). E) Normalized beta power during runs in the visual task with an aspect ratio low during perceptual reversals. Red represents the transition from the alternative perception to the dominant and grey represents the opposite reversal. F) Normalized beta power during runs in the visual task with an aspect ratio high during perceptual reversals. Blue represents the transition from the alternative perception to the dominant and grey represents the opposite reversal.

Expecting diferences in beta activity in the visual task with the ambiguous and bistable stimulus SAM, na unambiguous control for motor activity was initially divised. This control aims at removing ambiguity from the task which, should beta oscillations be related to perception under ambiguity (Minami et al., 2014, Costa et al., 2017), would also reduce beta activity. Moreover, given that motor preparation can also produce beta activity in 2-alternative forced choice paradigms (Little et al., 2019), this unambiguous task would also provide conditions to exclude a possible motor-related beta role.

The unambiguous SAM stimuli were physically similar in all aspects to the ambiguous SAM, differing only in having a constant aspect ratio of 1 irrespective of experimental condition and in that the two perceptual states of vertical and horizontal motion were elicited by a physically different configurations of the dots (see methods section; Figure 3.3). The unambiguous stimulus thus only produced real percepts of varying durations, which mirrored the durations perceived during the ambiguous task. Hence, runs biased towards horizontal motion corresponded to longer periods of the stimulus describing horizontal motion relative to vertical motion.

The time-frequency analysis for the unambiguous visual task show similar results to the ambiguous task. In time-frequency plots there is a decreasing in the power around the report of stimulus change (Figure 4.10A, B, C and D), especially in the beta (13-30Hz) and alpha band (8-10Hz). Analysing the time courses of beta power for all reports of stimulus change there is decrease just before and an increase after the moment that subjects reported the change (Figure 4.10E and F) but no significant differences between percepts was found ($p > 0.05$, nonparametric cluster-based statistic). This happens in both situations, from an alternative perception to a dominant perception, and vice-versa.

4.4.3. Beta activity during ABA perceptual changes

The figure 4.11 represent the results for the unambiguous visual task.

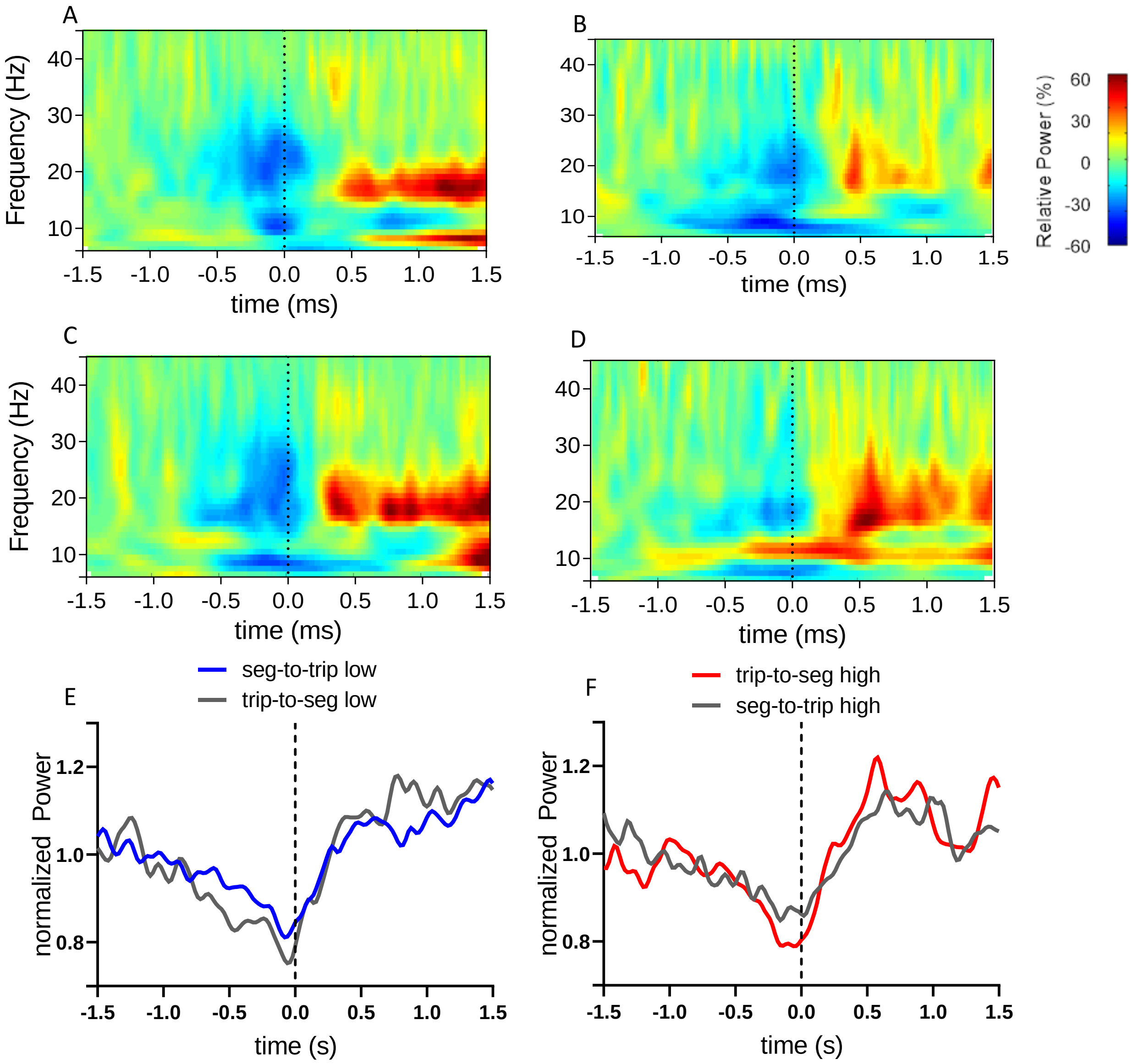

Figure 4.11 Results of the time frequency analysis in for the ambiguous auditory task. Images A, B, C and D represent spectrograms and the moment zero seconds represent the moment in which the observer reports a change. A) Spectogram of transitions segregated to grouped when the semitone difference is low (grouped perception is the dominant). B) Spectogram of transitions segregated to grouped when the semitone difference is high (grouped perception is the alternative). C) Spectogram of transitions grouped to segregated when the semitone difference is low (segregated perception is the alternative). D) Spectogram of transitions grouped to segregated when the semitone difference is high (segregated perception is the dominant). E) Normalized beta power during runs in the auditory task with a semitone difference low during perceptual reversals. Blue represents the transition from the alternative perception to the dominant and grey represents the opposite reversal. F) Normalized beta power during runs in the auditory l task with a semitone difference high during perceptual reversals. Red represents the transition from the alternative perception to the dominant and grey represents the opposite reversal.

A similar approach to the ambiguous task with SAM was carried out for an experiment engaging a distinct sensory modality: auditory bistability. This experiment intended on exploring the role of beta oscillations in influencing ambiguous perception not only originating from visual ambiguity, a particularly challenging question in the study of vision (Grassi et al., 2018), but also in auditory ambiguity (Curtu et al., 2019).

Two experimental conditions were set as previously described and resulted in auditory bistability with distinct dominant states. Epochs of perceptual reversals were obtained and analysed as with the SAM task, looking for differences in the spectral content that could be ascribed to either of the distinct percepts. The time frequency plots show that for either dominant or alternative changes there is a decrease of the power in beta band oscillations during a perceptual reversal (Figure 4.10A, B, C and D). After this, there is an increase in the same band of frequency, more noticed when the dominant percept is the grouped perception. Analysing the time courses of the beta band oscillations power (graphics E and F), there is a decrease before the reversal of perception during the auditory task, in both grouped-biased ABA and segregated-biased ABA. There is as well an increase of the activity of this band around 500msec after the subject reports the change in their perception. This increase seems to be substantially higher than the pre-reversal decrease, but it was not tested for differences between pre and post-reversal, having mainly focused on pre-reversal differences and post-reversal differences between perceptual conditions (e.g. grouped-to-segregated vs segregated-to-grouped).

4.4.4. General discussion

These results are not consistent with the hypothesis that was intended to prove, that there is an increasing of the power of beta band oscillations when after a reversal, the perception changes to a dominant configuration of the ambiguous stimulus. In fact, the results show that increasing exists, but it happens independently of the percept that the perception turns into. Our results, as previously said, might corroborate the theory that the beta band oscillations are related to the maintenance of the *status quo* and their activity decreases in a situation of changing the perception. This possibility is not fully proven by the results, because there always a dependency of motor response, that is already know that causes a decreasing in the activity of the beta band oscillations (Engel and Fries, 2010).

5. CONCLUSIONS AND FUTURE WORK

The role of beta oscillations is still a topic under much attention. Beyond its role in sensorimotor processing, beta oscillations have been suggested to also have cognitive functions (Spitzer and Haegens, 2017) particularly in mechanisms of top-down signalling (Arnal and Giraud, 2012).Beta activity related to ambiguity and bistability has been a recurrent finding in studies of bistable perception, particularly involving vision (Aissani et al., 2014, Minami et al., 2014, Zaretskaya and Bartels, 2015). In line with theories proposing beta as a main top-down signal, a crucial role of beta oscillations in perception could be of solving inherent ambiguities in sensory information. This could in fact explain many of the findings relating beta to a myriad of perceptual and cognitive mechanism that have been studied using bistable stimuli.

In this work, a study about bistable stimuli and beta oscillations was devised in order to assess whether beta activity is related to the perception of one specific percept when faced with ambiguous information. This hypothesis was first proposed by studies conducted by VanRullen et al (2006) and Piantoni et al (2010), both of which found a stronger power of beta band oscillations after a perceptual reversal towards the dominant percept. Although the kind of bistable stimuli used in the previously mentioned studies, frequently involving visual motion, was different from the ones employed in the present study there is no reason why such a recurrent finding couldn't also be generalized to most classes of ambiguous stimuli. For this reason, two stimuli were employed: one involving bistability in vision and the other in auditory modality. These stimuli were not selected by chance. In fact, while they engage distinct sensorial modalities, they share a common feature regarding the perceptual interpretation: both rely on interpreting information of stimulus-related activity over varying cortical distances. This is the result of the structured organization of the brain in cortical maps, more specifically the visual and auditory cortices, that represent physical differences between stimuli as physical distances in the cortex. In this way, both the visual and auditory stimulus can be seen as engaging on similar heuristics of cortical distance to interpret the most likely outcome of an ambiguous stimulus. From this angle, there is equivalency in the strategy of biasing both stimuli. One is biased by changing spatial relations between the flashing dots and the other by changing the spectral relation between the tones.

About the study of the ambiguous stimuli and the goal of bias them towards one specific perception instead of the other, the results were satisfactory. In the visual stimulus, it was always possible to achieve the expected dominance, while in the auditory one it failed just in one subject. The method used to bias the auditory stimulus was created by the researchers of this work, instead of the methodology used for the visual stimulus, which is a topic much more researched and with a vaster literature that helped in devising a reliable method. Regarding achieving specific percentages of viewing time of one perception, it is normal that sometimes it was not possible to recreate those specific percentages, because the experiment was performed in two different days, and factors such as attention and intrasubject variability could have played a role.

Although some preliminary tests were run to decide the methodology for the psychophysical part of the experiment, in the future it is better to dedicate even more time to this question to guarantee that the results obtained in the calibration part of the study have a larger probability to be reproducible. Mainly for the auditory streaming it is important to study a methodology to find the value of semitone difference which allow to the perception of segregated of a subject be perceived for 50% of the time.

The results obtained regarding beta oscillations did not show any specific increasing or decreasing of beta activity towards one percept, but rather as a standard occurrence when there is a perceptual reversal. A theory about beta band activity signalling the *status quo* (Engel and Fries, 2010) might justify the results of this experiment, but the need to use a motor response to report visual and auditory perception makes the results not enough proof to the theory .

In order to use the same data but having better results, in the future new analysis should be performed to verify more hypothesis, besides creating other experiments to bridge some flaws of this experiment. If it was used a single trial analysis of beta oscillations, it will be possible to study if in fact there is a variation in beta activity, which may actually manifest as bursts with high inter trial variability (Sherman et al., 2016).

In future studies, an effort to produce bistable figures with absolute durations more similar to other experiments could offer a more reliable approach.

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ANNEX A

Visual Stimulus – First Pilot

Preliminary tests were made to evaluate whether the contrast of the stimulus or the presentation frequency could affect the perceptual reversal rate of the bistable stimulus and which could be more appropriate for the present study. A pilot was created to be tested by two participants (both researchers working on the present study). This pilot consisted of 8 runs of 2min each of the visual stimuli for each participant. During this time participants continuously viewed the stimulus and reported their perception using two keys on a keyboard. Four runs were performed with a high contrast, i.e. black screen and white dots, and the remaining four runs with a lower contrast, grey screen and white dots. These two contrast conditions were combined with 4 different stimulus presentation duration, 433msec, 183 msec, 100 msec, and 67 msec, which represent a presentation frequency of, 1Hz, 2Hz, 3Hz and 3.73Hz, respectively, which correspond to 1 cycle, 2 cycles, 3 cycles and 3.73 cycles per second, respectively as well. It was not possible to produce a stimulus with a presentation frequency of 4Hz, because the duration of one cycle should be 250 msec, but this number is not divisible by the duration of one frame (16.67 mesc), so it is not possible to have 4 whole cycles in a second. The ratio of dimensions (width/height) of the stimulus was 1. As described before, participants continuously reported their perception by holding one of two buttons, representing a vertical and a horizontal motion, and were able to release both buttons in case of confusion.

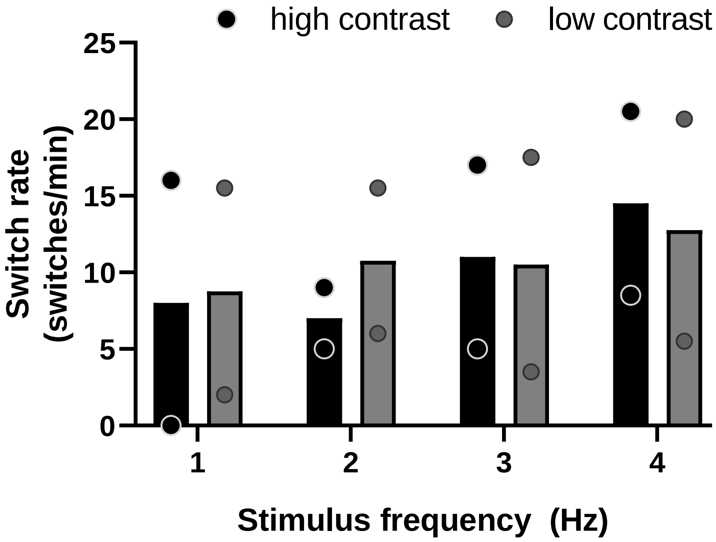

Figure A.1. Dependence of reversal rates on stimuli contrast and presentation rate. While the reversal rate increases with presentation rate, contrast conditions show no influence on the frequency of perceptual switches.

As shown in Figure A.1., there is a great variability in reversal rate that is related to intrasubject variability, observable at any of the tested conditions. Nonetheless, a clear trend toward an increase in the reversal rate with increased presentation rate can be observed. On the other hand, contrast does not seem to affect the bistable behaviour of the stimulus and hence was not further explored. The goal here was to set parameters for the stimulus within subject comfort and that would produce a more suitable set up for our task, mainly related to obtaining a sufficient number of events, i.e. reversals, for the analysis of the electroencephalogram data. It was decided that 2Hz of presentation frequency should provide a sufficient number of events (7.0±2.8 reversals/min over 12 min of recording for an average of 84 events per condition).

ANNEX B

Visual Stimulus – Second Pilot

After the first pilot of the visual stimulus, a second was performed to evaluate if a run of continuous stimulus viewing and perceptual report should last 1, 2 or 3 minutes. This pilot was done with the same two participants that performed the previous one. Each observer answered to one trial for each condition under the Method of Constant Stimulus (MoCS, see methods section 3.4.1) three times, one per trial duration wanted to be tested. Figure B.1 show the psychometric curves obtained for each condition.

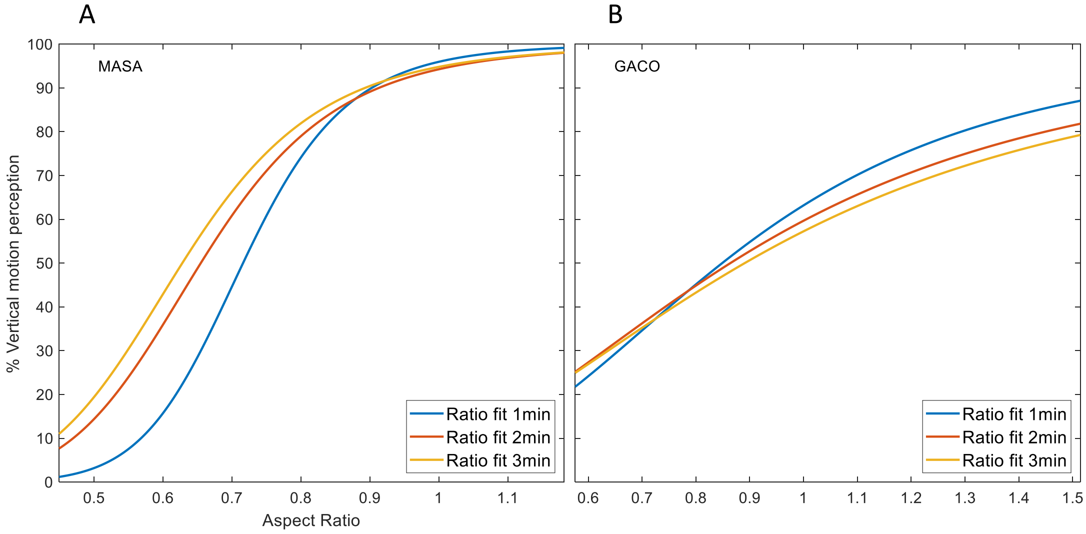

Figure B.1 Psychometric curves of the results of the second pilot for the visual stimulus. Each subject has three curves, one for each task duration testes (1, 2 or 3min). A) Results of the subject MASA. B) Results of the subject GACO.

In both participants, the psychometric curves changed according to the duration of the trial.

The figure B.2. presents the vertical motion dominance during the trials performed for 3 min.

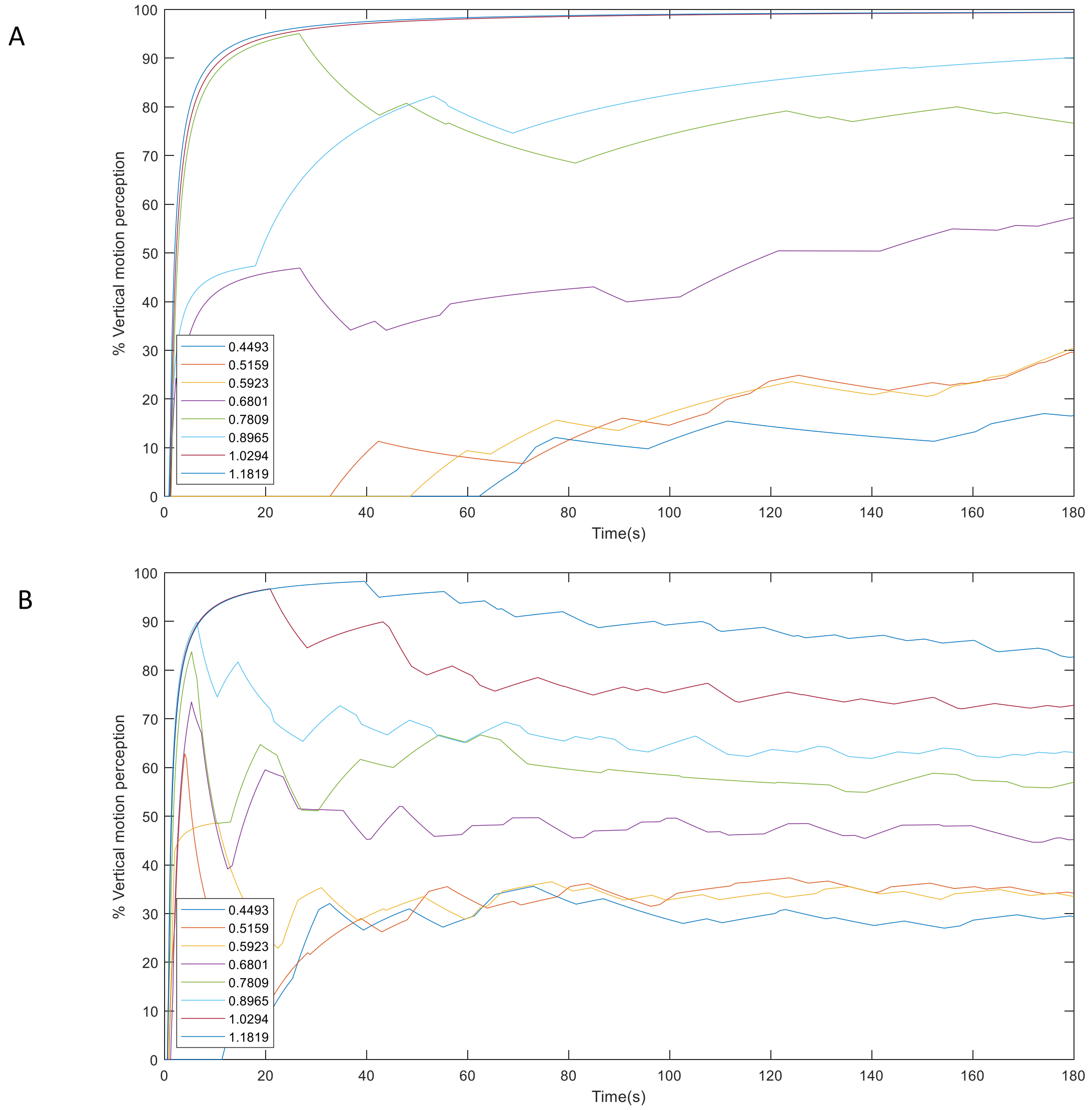

Figure B.2. Representation of the change of the vertical motion perception dominance during the trials in the second pilot for the visual stimulus. A) Results of the subject MASA. B) Results of the subject GACO.

In both participants the vertical motion dominance becomes steady or does not change considerably around 60 and 80 sec of trial. It was concluded that a trial should last more than 80s. Since an acquisition of EEG is a process that requires a lot of time for preparation and in order to make the most of an experiment, it was decided that the length of each trial would be of 3 min of visual stimulus.