FACULTY OF PSYCHOLOGY AND EDUCATIONAL SCIENCES

PERCEPTION OF BIOLOGICAL MOTION: AN EEG FREQUENCY TAGGING STUDY

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Elisabeth Loeys
Student number: 01807473

Supervisor: Dr. Cracco Emiel
Co-supervisor: Prof. Dr. Wiersema Roeljan

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Abstract

Humans are social creatures that need the ability to understand what others are doing and what their intentions are. Vision is an important source of information to perceive human movement. Several neuroimaging techniques have already been used to study the brain processes underlying biological motion perception. However, brain activity during motion perception consists of many different components. As a result, it is often unclear which components mark movement itself and which components reflect stimulus aspects independent of movement. The purpose of this study is to investigate whether biological motion can be measured with frequency tagging. Thirty participants performed a walker task where they saw a point-light walker walking at a frequency of 2.4 Hz (= 1 step per ~ 417 ms) while EEG frequency tagging was used to measure the brain response coupled to that pace. There were 4 possible conditions created by combining two manipulations: phase scrambling (unscrambled or scrambled) and inversion (upright or inverted walker). Our findings revealed two main effects. Firstly, we observed a significant main effect of scrambling, with stronger brain responses seen in the unscrambled condition compared to the scrambling condition. Additionally, we found a main effect of inversion, with stronger brain responses observed in the upright condition compared to the inversion condition. In addition to the main effects, an interaction effect was also found between scrambling and inversion, with a significant effect of inversion in the non-scrambled condition but not in the scrambled condition. These results indicate that frequency tagging can be used as a tool to measure biological motion perception.

Keywords: biological motion perception, EEG frequency tagging, point-light displays

Nederlandstalige samenvatting

Mensen zijn sociale wezens die het vermogen nodig hebben om te begrijpen wat anderen doen en wat hun bedoelingen zijn. Het gezichtsvermogen is een belangrijke bron van informatie om menselijke beweging waar te nemen. Verschillende neurobeeldvormingstechnieken worden reeds gebruikt om de hersenprocessen te bestuderen die aan de grondslag liggen van biologische bewegingswaarneming. De hersenactiviteit tijdens bewegingswaarneming bestaat echter uit veel verschillende componenten. Daardoor is het vaak onduidelijk welke componenten beweging zelf markeren en welke componenten stimulusaspecten weerspiegelen die onafhankelijk zijn van beweging. Het doel van deze studie is te onderzoeken of biologische beweging kan worden gemeten met frequency tagging. Dertig deelnemers voerden de walker-taak uit waarbij ze een 'point-light walker' zagen lopen aan een frequentie van 2,4 Hz (= 1 stap per ~ 417 ms) terwijl EEG frequency tagging werd gebruikt om de hersenrespons gekoppeld aan dat tempo te meten. Er waren 4 mogelijke condities gecreëerd door twee manipulaties te combineren: phase scrambling (niet-gescrambeld of gescrambeld) en inversie (rechtop of omgekeerde puntlichtloper). Onze bevindingen lieten twee hoofdeffecten zien. Ten eerste zagen we een significant hoofdeffect van scrambling, met sterkere hersenresponsen in de niet-gescrambelde conditie vergeleken met de gescrambelde conditie. Daarnaast vonden we een hoofdeffect van inversie, met sterkere hersenresponsen in de rechtopstaande conditie vergeleken met de inversie conditie. Naast de hoofdeffecten werd ook een interactie-effect gevonden tussen scrambling en inversie, met een significant effect van inversie in de niet-gescrambelde conditie maar niet in de gescrambelde conditie. Deze resultaten geven aan dat frequency tagging gebruikt kan worden als instrument om biologische bewegingswaarneming te meten.

Sleutelwoorden: biologische bewegingsperceptie, EEG frequency tagging, point-light displays

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1. Introduction

The recognition of complex movements and action is a biological need of every living organism. Indeed, human beings are social creatures so, therefore, it is crucial that they have the ability to understand what others are doing and what their intentions are; not only through verbal communication but also through non-verbal avenues such as gestures and expressions. To perceive human movement, vision is a rich source of information. Perception of human actions promotes our social needs by picking up socially relevant information and thereby facilitates more effective social interaction. In this introduction, I will provide an overview of studies that have contributed to the understanding of the visual processing of human movement. This will be followed by a discussion of the neuronal system underlying the perception of biological motion.

1.1 Visual perception of human motion

From our daily experience, we know that we can visually distinguish a large number of different details in movement patterns. Indeed, we can distinguish between when a person is walking, running, or jumping and at what speed a person does so. All this information enters the visual field. It is processed by the visual system, a large and complex but well-organized entity. The purpose of the visual system is to construct an internal model of the external world that can then serve as the perceptual basis for all visually derived thoughts and actions. The human brain has two primary pathways for visual processing, the retino-collicular pathway and the retino-genicular pathway, based on where they end in the subcortex. The retino-genicular pathway is the basis for two separate cortical processing streams for visual inputs: a ventral stream for the visual recognition of objects ("what" an object is) and a dorsal stream for processing the spatial relationships between objects and the visual guidance to them ("where" and "how" an object is) (Mishkin & Ungerleider, 1982). The ventral pathway runs from V1 (striate cortex) through areas V2 and V4 (prestriate cortex) to the inferior temporal cortex and to the anterior part of the superior temporal sulcus (STS). The dorsal route runs from V1 through areas V2 and V3 to the middle temporal area (V5/MT) and from there to the superior temporal and parietal cortices.

Mishkin and Ungerleider (1982) provided a theoretical framework that maps behavioral functions (the "what," "where," and "how" of an object) to visual pathways. This framework paved the way for much later research on the mechanisms of vision. More specifically, it provided a framework for distinguishing the recognition (ventral pathway) and localization (dorsal pathway) of objects (Goodale & Milner, 1992). After many years of research, Pitcher and Ungerleider (2021) have now also shown that there is a third pathway. While the ventral and dorsal pathways deal with the "what", "where", and "how" of visual object recognition, the third

pathway is primarily involved in processing biological motion (Pitcher & Ungerleider, 2021). Biological motion perception is the ability of the visual system to perceive human motion effortlessly and within a fraction of a second (Lange & Lappe, 2006). The processing of biological motion happens at different levels. On the one hand, you have brain regions early in the pathway (such as MT) that are involved in processing basic motion (speed discrimination or detection of coherent motion), but further upstream you have regions (such as the STS) that specifically focus on processing biological motion. The specialized low-level motion detection system operates at very short time intervals and processes changes in the image that occur within a time span of about 50 ms. The higher-level process can operate over a much longer interval, up to about 500 ms. Pitcher and Ungerleider (2021) review the studies which showed that biological movement (e.g., facial and body movement) drives the neural response to visual stimuli in the STS and find evidence that the third visual pathway is anatomically and functionally distinct from the ventral and dorsal visual pathways.

The third visual pathway outlined by Pitcher and Ungerleider (2021) corresponds to what models of biological motion perception call the structure-from-motion pathway or motion pathway, where perception of biological motion arises from an analysis of the kinematics of observed movements (Giese & Poggio, 2003; Lange & Lappe, 2006). This pathway consists of a hierarchy of neural detectors for motion features of increasing complexity. The detectors at the beginning of the pathway process local motion cues and the detectors further along the motion pathway are integrated into a global motion perception. In addition, there is also another pathway, namely the motion-from-structure path or shape path, in which biological motion perception arises from combining sequences of static body snapshots into fluid motion. The shape path is actually an expanded version of the model of object recognition. This path involves a hierarchy of neural detectors that process shape features of increasing complexity. Thus, although the motion pathway is not the only pathway relevant to biological motion, it is the most important pathway because it is the only pathway that actually processes motion. This research will therefore focus on this pathway.

Building on these findings, a number of different methods have been developed to study biological motion perception. Johansson (1973) developed a method, “the point light” technique, for studying biological motion perception in the structure-from-motion pathway. Different types of human movement, i.e., running, dancing, jumping, etc., are all composed of combinations of specific motion patterns characteristic of the different types of movement. With the point-light technique, the activity of a human is portrayed by the relative motions of a few ($\pm$ 10) markers positioned on the head and the joints of the body (see **figure 1**). By representing human movement through this technique, shape information is eliminated, obtaining a relatively pure measurement of movement perception.

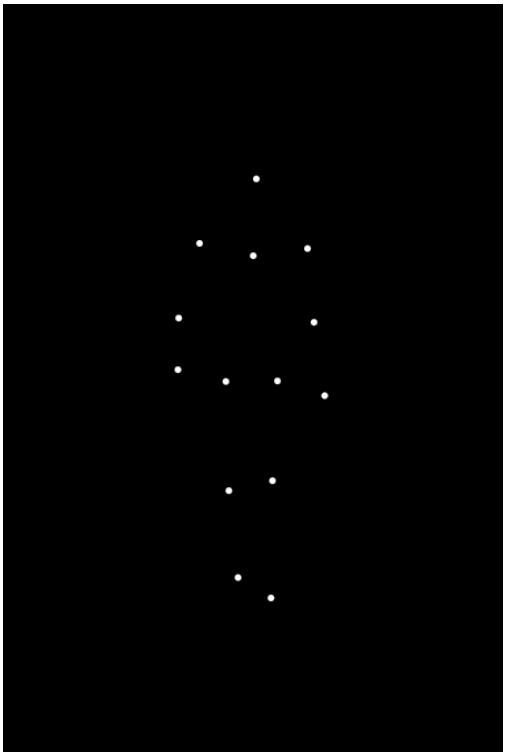

Figure 1. *Point-Light Walker.*
(Biomotionlab. Retrieved May 19, 2022, https://www.biomotionlab.ca/Experiments/BMLstimuli/index.html)

Several studies have demonstrated how the point light (PL) technique can be used to measure biological motion perception (Blake & Shiffrar, 2007). Observers can easily recognize which movement is depicted in a point light display (PLD), even though there is a wide range of possible activities (e.g., Dittrich, 1993; Norman et al., 2004). Human motion is most visible when the lights are placed on the joints of the body, but it can also be recognized when the lights are placed on other parts of the body (Bertenthal & Pinto, 1994). Even under poor or potentially ambiguous conditions, the perception of human motion is remarkably robust (Neri et al., 1998; Poom & Olsson, 2002; Thornton et al., 1998; Bertenthal & Pinto, 1994; Cutting et al., 1988; Ikeda et al., 2005). When viewing PL animations, the observers could estimate the emotional implications of an action based on the entire body (Clarke et al., 2005; Dittrich et al., 1996; Walk & Homan, 1984) or a specific limb (Pollick et al., 2001). Emotional expression can also be identified when PL faces are shown (Bassili, 1978).

Despite the fact that the processing of PLDs is quite robust, there are two manipulations that disrupt it, namely scrambling and inversion. Both manipulations are known to interfere with the perception of biological motion. Scrambling is achieved by scrambling components to make the perception of the original signal more difficult. There are two types of scrambling. The first type is phase scrambling, where each dot is manipulated to start at a different point in the motion cycle. By scrambling the phase, the different dots are no longer aligned. This makes the movement look unnatural and harder to recognize. The other type of scrambling is spatial

scrambling where the location of the lights is mixed up. When the elements of a PLD are spatially intermingled, so that the contour of the elements no longer corresponds to a human figure, the impression of a human or animal form is greatly reduced (Pinto & Shiffrar, 1999). The other manipulation is inversion, in which the PL walker is presented upside down. People have difficulty perceiving PL animations when they are shown upside down. Reed et al. (2003) found that distinguishing two upright body postures is much easier than distinguishing two inverted body postures. Based on these findings, it can be argued that our frequent perception of other bodies results in a kind of visual expertise (Bosbach et al., 2006). Indeed, during visual processing, perceptual input is mapped onto a spatial representation that captures specific structural relationships present when observing other bodies. This allows frequent observation of bodies to discern specific configurational relationships that are present in human bodies. These relationships are disrupted when the body is presented upside-down. This implies that people cannot easily mentally rotate images (Pavlova & Sokolov, 2000). However, with practice, observers can learn to detect inverted human movements. In doing so, observers rely on the detection of distinctive clusters of points, not on the general impression of a human figure (Hiris et al., 2005). This demonstrates the use of "configural processing," where the perception of biological motion relies on interactions between different components of that motion.

1.2 Neural mechanisms underlying the biological motion perception

However, although behavioral research has already taught us much about biological movement perception, it can never provide a pure measurement of movement perception because movement processing is always inferred indirectly from performance on a task (i.e., participants are usually asked to actively search for a PL figure in noisy displays). To analyze biological motion processing directly, we can use neuroimaging methods. Several neuroimaging techniques have been developed to study the brain processes underlying biological motion perception. Two commonly used techniques to do this are fMRI (functional magnetic resonance imaging) and EEG (electro encephalogram).

The results of several neuroimaging studies indicate the existence of neural mechanisms specialized in the analysis of the kinematics that determine biological motion. These specialized neural mechanisms work together in a coordinated manner, integrating and relaying information to the visual pathways that map the behavioral functions (the "what," "where" and "how" of an object). fMRI studies have shown that in processing biological motion, the extra-striate and fusiform body regions, the MT and the STS play an important role, each of which in turn fulfills a different function. Several studies found that particularly the posterior region in the STS (STSp) in the right hemisphere responds strongly to human movement (Beauchamp et al., 2003; Grossman et al., 2000; Santi et al., 2003; Peuskens et al., 2005). Peuskens et al. (2005) and Grèzes et al. (2001) found that the MT is active when a complex motion pattern is present in

the biological motion rather than that the figure or action itself activated this region. The extrastriate body area (EBA) is activated when viewing human bodies or isolated body parts. Activation of the EBA does not require movement unlike the STSp or MT, but body movements can cause strong responses in the EBA (Downing et al., 2001). Activity in all of these brain regions is reduced by manipulations, such as scrambling (Grossman et al., 2000; Peuskens et al., 2005) and inversion (Grossman & Blake, 2001; Pavlova et al., 2017; Peuskens et al., 2005), which interfere with biological motion perception.

EEG testing looked at the electrical activity in the brain that was elicited during the viewing of biological motion. White et al. (2014) showed that scrambling and inversion have similar effects but occur at different stages of processing. Scrambling already has an effect from 150-200 ms, while the inversion effect only emerges from 400 ms. In an event-related potential (ERP) study by Hirai et al. (2003), subjects were shown biological motion or scrambled motion as a control stimulus. In the scrambled motion, all points moved with identical velocities to the biological motion, but their starting positions were randomized. The perception of both biological and scrambled motion resulted in negative peaks at approximately 200 (N200) and 240 ms (N240). These negative peaks were significantly larger in the biological motion condition compared to the distorted motion condition over the right occipitotemporal region. Therefore, it is assumed that component N200 is generated near the extrastriate cortex area and N240 is generated from the area of the STS.

Both fMRI and ERP studies have enhanced knowledge about biological motion perception tremendously. However, a drawback of existing EEG and fMRI studies is that even though they measure brain activity during biological motion perception, they do not necessarily measure movement processing per se. Other processes such as inferring identity or gender based on movements also take place during biological motion perception (White et al., 2014; Cutting & Kozlowski, 1977). One method that does allow us to measure brain activity specifically linked to movement processing is EEG frequency tagging (EEGft). This method allows us to unravel the respective neural responses elicited by different streams of stimuli. Unlike the other neuroimaging techniques, EEGft does allow us to reveal which aspects of the brain response specifically reflect visual movement processing and which aspects represent secondary processes associated with biological motion processing, such as familiarity, size and shape cues, or other sources of information such as likelihood of seeing a person at a particular place or time (Cutting & Kozlowski, 1977).

1.3 EEG frequency tagging method

The principle of EEGft is very simple. Presenting stimuli at a fixed rate generates a periodic EEG response with exactly the same frequency, known as a steady-state visual evoked potential (SSVEPs, Regan, 1966, 2009). A good example is the study Rossion et al. (2012). In

this study, the researchers used the SSVEP approach to measure the brain's response to a series of periodic faces presented at a frequency of 4Hz and manipulated the parameters of the stimuli (e.g., contrast and orientation) to study their impact on the brain's response. The results showed that presenting faces at 4Hz elicited a brain response at 4Hz that was modulated by the manipulations of contrast and orientation, known to influence face perception. This shows that frequency tagging is a valuable technique to isolate the processing of a specific visual stimulus (in this example: faces). By presenting the stimulus at a fixed frequency, the neural activity related to the processing of that stimulus can be analyzed by examining the signal at that frequency.

EEGft has two major advantages (Norcia., 2015; Alp et al., 2016; Figueira et al., 2022). First, EEGft has a very high stimulus-to-noise ratio because the brain response is limited to a very narrow frequency band. As a result, high power can be obtained with a relatively small sample size and short experiments. Second, SSVEPs allow the use of highly selective frequency markers that obtain an objective measure of stimulus processing due to the direct link between stimulus and response. More specifically, the brain's response can be synchronized with a repetitive movement like walking. Consequently, the brain generates a recurring response that corresponds to each instance of the movement. This synchronization effectively isolates the processing of the movement itself from other concurrent processes that may occur during movement perception but are not directly linked to the movement. In this way cyclical brain responses are evoked that align with the repetition rate of the movement.

Frequency tagging has already been applied in several domains. It has been used to assess lower sensory processes in infants, such as orientation selectivity (Braddick et al., 1986; Hamer & Norcia., 1994), as well as to examine higher visual processes, such as face processing (Barry-Anwar et al., 2018; Buiatti et al., 2019; de Heering & Rossion, 2015; Farzin et al., 2012; Peykarjou et al., 2017; Vettori et al., 2020) and the processing of unexpected events (Köster et al., 2019). However, despite successful applications in a wide range of visual domains as mentioned above, only few studies have used frequency tagging to study movement processing.

1.4 EEG frequency tagging and biological motion perception

In the study conducted by Alp et al. (2017), PLDs depicting human movement were presented to participants in a way that changed the contrast of the stimuli at fixed frequencies. This allowed the researchers to use EEGft to isolate neural processes that were associated with those specific frequencies. In other words, this study studied contrast processing in the context of biological motion processing using EEGft. In a study by Zarka et al. (2014) they used frequency tagging to investigate the neural oscillations in different frequency bands (theta, alpha, beta, and gamma) during observation of human walking under two conditions: upside-

down and uncoordinated. Frequency tagging can also be used as a method to measure the attentional focus of participants while they are viewing biological motion stimuli (Hasan et al., 2017). Hasan et al. (2017) used SSVEPs to measure the neural response to flickering stimuli superimposed on the biological motion displays. By varying the frequency of the flickering stimuli the authors were able to track changes in the participants' attention to different parts of the biological motion displays and to determine the extent to which attention was focused on different features (such as the movement of the head or limbs). Thus, biological motion processing was already combined with frequency tagging. However, these studies never tagged the movement itself, but rather tagged stimulus aspects independent from the movement (e.g., stimulus contrast in Alp et al., 2017).

In this study, we take a different approach and tag the movement itself to measure biological motion processing. That is, the purpose of the current study is to investigate whether we can effectively use frequency tagging to measure biological motion perception. By presenting a point light figure walking at a specific frequency, we will measure brain responses associated with this frequency. As such, we expect that cyclic brain responses will be elicited that are linked to the fixed rate at which motion is repeated. As this brain activity is locked to movement frequency, movement processing is separated from other processes that also occur during motion perception but are not specifically linked to the movement itself. Therefore, if successful, our approach will provide an objective measurement of movement processing.

In order to verify whether biological motion can be measured with frequency tagging, we will manipulate two variables that are known to interfere with biological motion perception, namely phase scrambling (Beintema et al., 2006; Troye & Westhoff, 2006) and body inversion (Bertenthal & Pinto, 1994; Pavlova et al., 2017; White et al., 2014). We hypothesize that visual processing of biological motion can indeed be measured by frequency tagging and hence that the brain response linked to the walking frequency will be lower when the walker is scrambled or presented upside down.

Open science statement

This study was preregistered (https://aspredicted.org/blind.php?x=1P9_PNW).

2. Method

2.1 Participants

Before recruitment, a power analysis was performed. Since this is the first study to use frequency tagging to measure the processing of biological motion with PL stimuli, we had no previous studies to rely on regarding effect size. Given that scrambling and inversion typically have fairly strong effects (e.g., Bertenthal & Pinto, 1994; Grossman et al., 2000; Grossman & Blake, 2001), it seemed like a safe and conservative estimate for us to choose a medium effect size. As such, we calculated the sample size that would be needed to detect an average effect of d=0.50 (power = 0.80): this resulted in 33 participants. However, after testing the preregistered 33 participants, we found an undetected technical problem with 9 participants. We compensated 6 participants so that we could obtain a final sample of 30 participants (as pre-registered), of which 10 males and 20 females (M_{age} = 23.03, $range_{age}$ = 18–33). The participants were recruited via SONA, a platform of the UGent-FPPW. Exclusion criteria included: history of neurological or psychiatric disorder, epilepsy (in participant or family history), dreadlocks/cornrows, and disease symptoms that could indicate COVID-19 in the last 14 days. Furthermore, participants had to be between 18-35 years of age and had normal or corrected-to-normal vision. The study took place at the Faculty of Psychology and Educational Sciences, Ghent University. Each participant signed the informed consent at the beginning of the study and received a compensation of 25 euros after participation. The research was approved by the ethical committee of the Faculty of Psychology and Educational Sciences, Ghent University (2021/129).

2.2 Equipment, task & procedure

Before coming to the laboratory, the participant was asked to provide their head circumference so that preparations for EEG recording went smoothly. In the laboratory, the setup of the chamber was explained to the participant, and they were asked to remove all electronic devices from the Faraday cage. Before the experiment began, everyone was given explanations about the informed consent form. After this was completed and signed, the specific task (i.e. the walker task) that participants had to perform was explained. Meanwhile, a suitable electrode cap with 64 electrodes was chosen and mounted according to the 10% system. During the experiment, the participant sat in a Faraday cage at a distance of 80-100 centimeters from a 24-inch screen. The experiment was programmed in PsychoPy. The entire study, which also included experiments not reported here, lasted about an hour.

The walker task consisted of 16 blocks of ~ 52 sec each. In a single block the participants saw a point-light walker walking at a frequency of 2.4 Hz (= 1 step per ~ 417 ms, see **figure 2**). Each trial began with a fade-in period of ~ 4 sec in which the contrast of the stimulus was gradually increased from 0 to 1 and ended with a fade-out period of ~ 4 sec in which the contrast of the stimulus was gradually decreased from 1 to 0 (0 contrast means that the stimulus is invisible). All point-light walkers were displayed in white dots against a black background. The point-light figures were created using the online BMLStimuli tool (https://www.biomotionlab.ca/Experiments/BMLstimuli/index.html). There were 4 possible conditions (see **figure 3**) created by combining two manipulations: scrambling (unscrambled or scrambled) and inversion (upright or inverted walker). The specific type of scrambling manipulation was a temporal (= phase) scrambling manipulation. This means that the start frame was randomly determined for each individual dot in the scrambled condition, making them uncoordinated. Each of the 4 conditions was repeated 4 times (1 condition per block). To limit habituation effects and to provide some variation, though, the exact stimulus was also variable. There were 4 types of stimuli: man or woman and either walking left or right. Each stimulus occurred 1 time per condition (4 conditions x 4 stimuli = 16 blocks). The middle dot of the walker was colored gray. Participants' task was to look at that gray dot and press the space bar each time it turned red (2 to 4 times per block). This was purely to keep participants' attention and led to an accuracy on this task of 97-98% in all conditions.

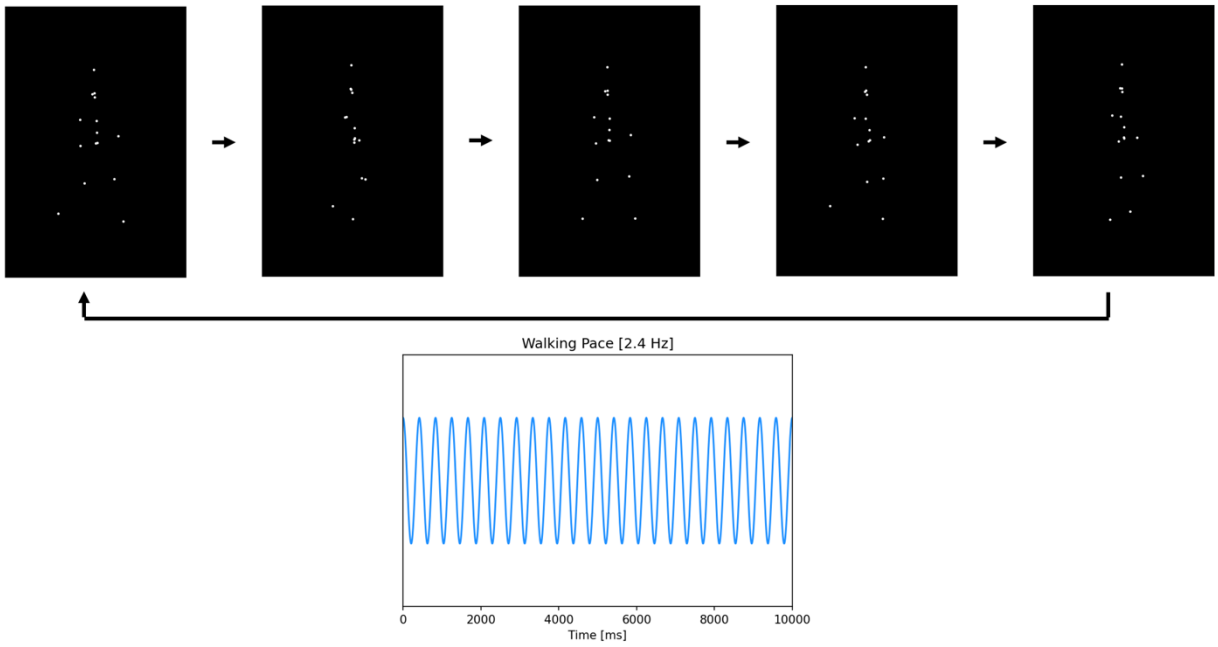

Figure 2. *Experimental task.*

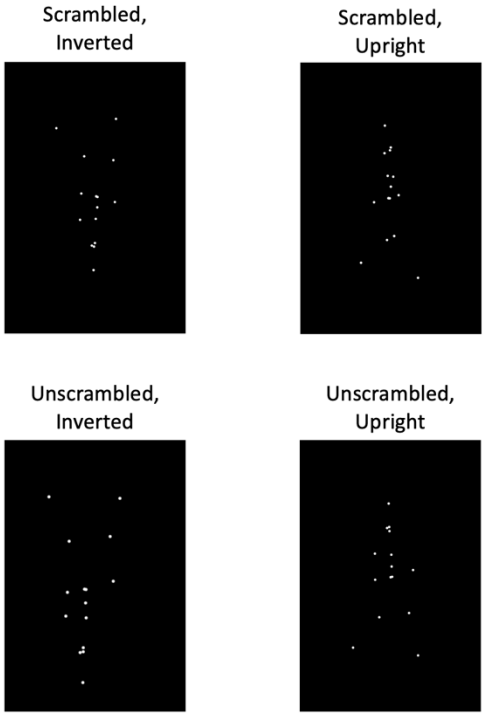

Figure 3. *Four conditions of 2 × 2 repeated measures design.*

2.3 Preprocessing

EEGft was recorded from 64 Ag/AgCI active electrodes at a sampling rate of 1000 Hz using an ActiCHamp amplifier and BrainVisionRecorder software (version 1.21.0402, Brain Products, Gilching, Germany). Electrodes were mounted according to the 10% system except for two electrodes (TP9 and TP10), which were placed on OI1h and OI2h according to the 5% system so that better coverage of the posterior scalp sites could be obtained. Fpz was used as ground electrode and Fz was used as online reference. Vertical eye movements were recorded using two additional bipolar AG/AgCI sintered ring electrodes placed above and below the left eye. Horizontal eye movements were recorded using the FT9 and FT10 electrodes embedded in the EEG cap.

Offline processing of the EEG signal was done using Letswave 6 (www.letswave.org) based on the following steps. As a first step, the raw data were filtered using a fourth-order Butterworth filter with 0.1 Hz and 100 Hz as cut-off values. The filtered data were then segmented according to the 4 experimental conditions (-2 to 54 s). An independent component analysis (ICA; RUNICA algorithm, square mixing matrix) was then applied to the merged segmented data to remove ocular artifacts. The first 10 components were inspected and components that captured eye blinks or horizontal eye movements were removed. After ICA, defective or excessively noisy electrodes were interpolated from the 3 nearest neighbors (average 2%, never more than 10%).

Fz was added again, and data were rereferenced to the average signal across all electrodes. Then the data, were cut into epochs running from the end of the fade-in to the beginning of the fade-out period so that the epoch length was a multiple of the presentation rate. As a final step, conditions were averaged and a Fast Fourier Transform algorithm was used to calculate the discrete Fourier transform of the signal, converting it to normalized (divided by N/2) amplitudes (μV) in the frequency domain (Cracco et al., 2022).

2.4 Data-analysis

In frequency tagging, a response is evoked not only at the tagged frequency but also at the harmonics of that frequency. Since the brain signal is dispersed over these harmonics, the amplitudes of the harmonics should be summed to capture and describe the brain signals as a whole (Norcia et al., 2015; Retter et al., 2021). To determine how many harmonics to include, the signal was averaged across conditions, electrodes, and participants. Next, a z-score was calculated for each frequency bin that summarizes how strong the signal is at that frequency relative to the 20 surrounding bins (excluding the directly adjacent bins). Harmonics with $z > 2.32$ ($\sim p < .01$, one-tailed) were included. This procedure identified three relevant harmonics (2.4 Hz, 4.8 Hz, and 7.2 Hz) for this study. For each of these 3 harmonics, the brain signal was quantified by calculating for each the difference between the amplitude at the harmonic frequency itself and the 20 surrounding frequency bins (again excluding the directly adjacent bins). Then these three baseline-subtracted amplitudes were summed (Retter et al., 2021).

To determine which electrodes to use, the collapsed localizer approach (Luck & Gaspelin, 2017) was used. This involved creating a topography of the brain signal from each electrode averaged across participants and conditions. Based on the activation clusters that appeared in this topography, electrodes were chosen. There was activity **(Figure 4)** in all occipital, parieto-occipital and parietal scalp locations, noting that activation tended more to the right. Because this was consistent with what is typically found in biological motion perception research (Grossman et al., 2000), namely right lateralization, we decided to include hemisphere as a factor in the analysis. We did this by ignoring the middle electrodes and creating two clusters: one left and one right. However, similar results were found when the middle electrodes were also included. Finally, we calculate the mean brain signal for each participant, condition and cluster and put those data into a repeated measure ANOVA with scrambling (scrambled vs. non-scrambled), inversion (inverted vs upright), and laterality (left vs right) as within-subject factors.

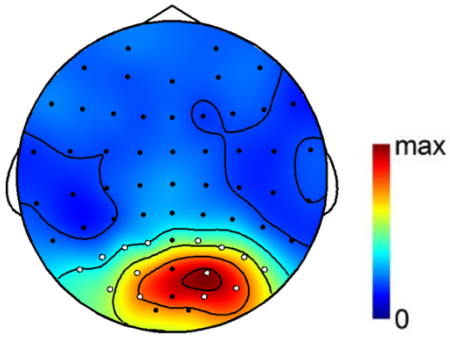

Figure 4. *Topography of the brain signal. Electrodes included in the analysis are indicated in white.*

3. Results

Analyses of brain responses (**figure 5**) associated with the 2.4 hz frequency revealed three main effects. First, there was a main effect of scrambling F (1, 29) = 45.64, p < 0.001, with stronger brain responses in the unscrambled condition compared to the scrambled condition. Secondly, a main effect of the inversion condition, F (1, 29) = 5.36, p = 0.028, with stronger brain response in the upright condition relative to the inversion condition. Thirdly, there was also a main effect of lateralization, F (1, 29) = 12.30, p = 0.001, the right hemisphere has a stronger brain response compared to the left hemisphere (**figure 6**).

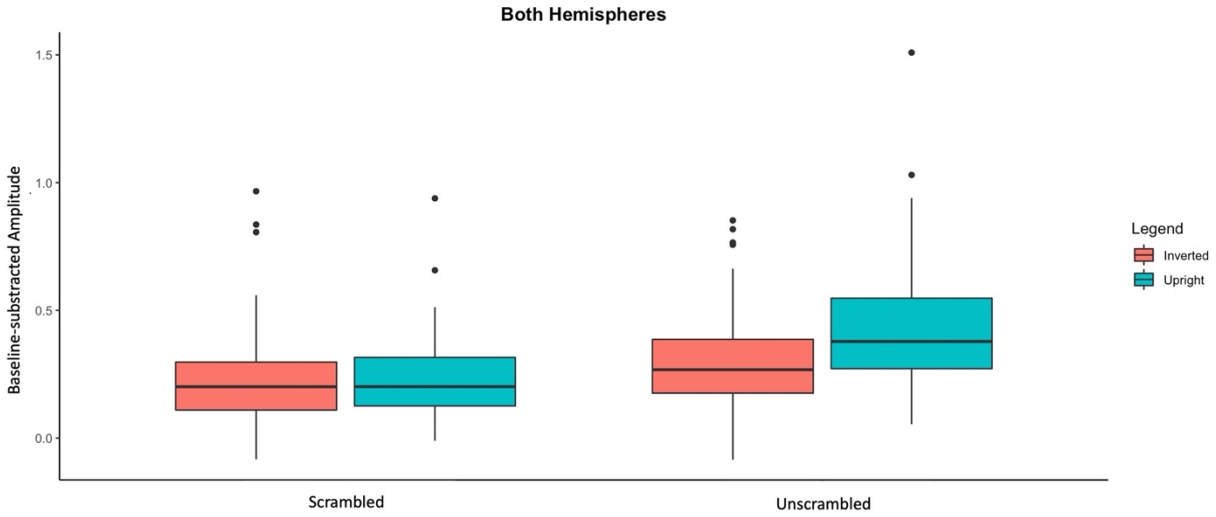

Figure 5. *Boxplot of Baseline-Substracted Amplitudes at 2.4 Hz and Harmonics for whole brain.*

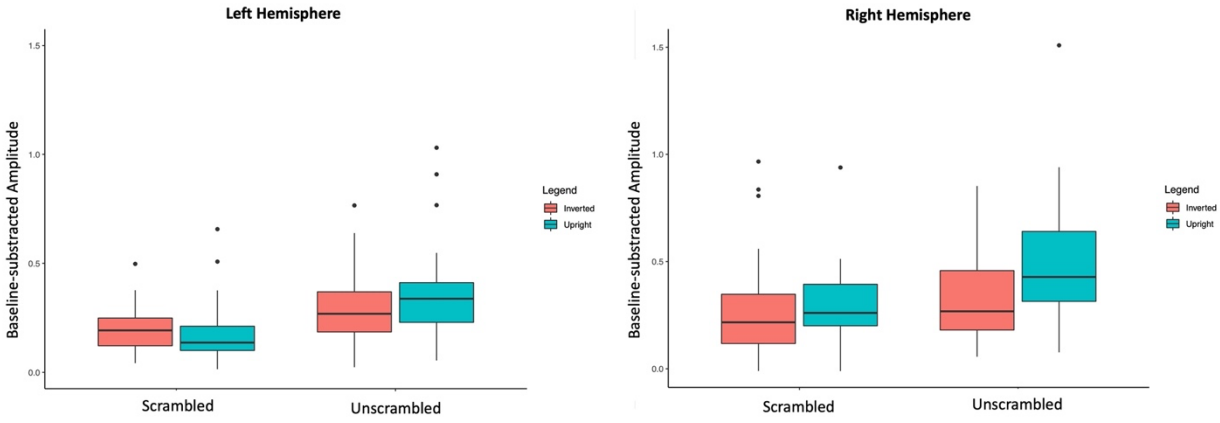

Figure 6. *Boxplot of Baseline-Substracted Amplitudes at 2.4 Hz and Harmonics for left and right hemisphere, respectively.*

In addition to the main effects, an interaction effect was also found between scrambling and inversion conditions, F (1, 29) = 8.50, p = 0.007, with an effect of inversion in the non-scrambled condition, F (1,29) = 9.5, p = 0.004, but not in the scrambled condition, F (1,29) = 0.223, p = 0.640. The other interaction effects were not significant, all F ≤ 2.04, all p ≥ 0.164.

4. Discussion

In this study, we investigated whether we can effectively use frequency tagging to measure biological motion perception. We did this using a walking point light figure at a frequency of 2.4 Hz. There were 4 possible conditions created by combining two manipulations, scrambling (scrambled or unscrambled: Beintema et al., 2006; Troye & Westhoff, 2006) and body inversion (inverted or upright: Bertenthal & Pinto, 1994; Pavlova et al., 2017; White et al., 2014). These manipulations are known to disrupt biological motion. We hypothesized that the brain response associated with walker motion would be lower when the walker is scrambled or presented upside down.

We found that there was a main effect of scrambling with stronger brain responses in the unscrambled condition compared to the scrambling condition. In addition we also found a main effect of inversion, with stronger brain response in the upright condition relative to the inversion condition. Apart from the main effects, there was also an interaction effect between scrambling and inversion. Specifically, the effect of inversion was significant in the non-scrambled condition but not in the scrambled condition. These results confirm our hypothesis and provide support that frequency tagging can be used as a tool to measure biological motion perception.

Previous research has already combined biological motion processing with frequency tagging. However, in these studies, frequency tagging was not used to tag the movement itself, but rather to tag stimulus aspects that were independent of the movement, such as contrast in the study by Alp et al. (2017). This study used EEGft to distinguish and isolate the brain's response that is specifically associated with movement. From the results of this study, we can conclude that frequency tagging allows for the separation of biological motion from other cognitive processes that may occur during the perception of movement but are not directly tied to the movement itself. Frequency tagging thus can be used as a full-fledged tool to tag movement itself to measure biological motion processing.

The present findings may be theoretically and clinically relevant. Firstly, in a study from 2009, Chang and Troje explored the different ways in which we process biological motion. They discovered that we perceive it on two levels: either locally, as a collection of moving dots, or globally, as a single moving agent. By oscillating local and global stimulus features at different frequencies, it could be explored in the future to see if frequency tagging can disentangle them within the same stimulus. In addition, our research using EEGft in the study of biological motion processing can offer new insights into the underlying neural mechanisms that support the perception of biological motion. By presenting stimuli at specific frequencies, researchers can identify which neural networks are active during different phases of processing, thereby providing a detailed understanding of the temporal dynamics of biological motion processing. There is some evidence that the brain response is generated by lower-order areas when

working with high frequencies and by higher-order areas when working with low frequencies (Cottereau et al., 2011; Alonso-Prieto et al., 2013; Norcia et al., 2015). Future research with frequency tagging can help us understand how various neural regions work together to extract directional movement information from PLDs, and how other cognitive and perceptual processes such as attention or emotion affects this. Despite not being able to pinpoint the exact brain regions involved in this process, EEGft provides valuable information about the coordination and timing of neural activity across different regions. Furthermore, it may also help to understand the neural mechanisms of developmental disorders like autism spectrum disorder (ASD), where biological motion processing is known to be impaired (Federici et al., 2020; Van der Hallen et al., 2019). Although there is mixed evidence, Van der Hallen et al. (2019) reported a small deficit in global motion processing in individuals with ASD compared to controls in biological motion. The inconsistency in the findings may be due to the entanglement of local and global processes in most biological movement tasks as suggested by Chang & Troje (2009b). Our research demonstrates that frequency tagging offers an objective tool to measure biological motion processing, making our study a valuable contribution to this ongoing debate. Researchers may gain a better understanding of the specific aspects of biological motion processing that differ between individuals with and without ASD. This could provide valuable insights into the neural mechanisms underlying ASD and potentially inform the development of new diagnostic and therapeutic approaches. Another potential clinical implication of studying biological motion processing met frequency tagging is its application in the study of recovery from brain injury or stroke. By a brain injury or stroke, disruptions in biological motion perception can occur depending on the location and extent of the damage to the brain (Urgesi et al., 2014). When these regions are affected, it disrupts the ability of the visual system to perceive and interpret the movements of living organisms. The specialized visual processing mechanism that allows us to recognize and understand the actions, intentions, and emotions of others based on their body movements is affected. By using an objective measure to observe biological motion researchers can gain valuable insights into the brain's ability to adapt and recover following injury, ultimately leading to better treatment and rehabilitation strategies for patients with brain injury or stroke. However, more research is needed to fully understand the clinical implications of EEGft for biological motion processing.

This study has also limitations. The main disadvantage of EEG recording is its poor spatial resolution. The EEG waveform does not distinguish between activities originating in different but close locations and therefore cannot reveal which brain regions are involved in processing biological motion. Thus, EEG research is not useful to pinpoint the exact source of activity because of its low accuracy. In future research, EEG and fMRI can be combined in a technique called simultaneous EEG-fMRI for measuring biological motion processing. This technique allows for the simultaneous recording of neural activity from the scalp (using EEG) and brain

activity (using fMRI). By combining EEG and fMRI, researchers can take advantage of the high temporal resolution of EEG and the high spatial resolution of fMRI to gain a more complete understanding of neural activity during biological motion processing. In addition, the current study examined only one type of scrambling, namely temporal or phase scrambling. Further research will have to show whether spatial scrambling has similar effects. Third, this study uses only one movement form namely, walking. Even though walking is the most commonly used movement pattern in research, future research will have to show if other movement patterns can be studied whether or not with frequency tagging. Fourth, the sample size is relatively small with 30 participants included. Although we had predicted to have 80% power for detecting d=0.5, it will be interesting to replicate our findings in a larger cohort with larger a priori d-values. Finally, it is unclear whether the findings of this study would be applicable to other frequencies as only one frequency (2.4 Hz) was used. Further research is needed to explore the extent to which similar results would be obtained with different frequencies.

Despite these limitations, this is the first EEG frequency tagging study to tag movement itself to measure biological motion processing. Measuring biological motion perception with frequency tagging provides several important advantages for future research. First, compared to fMRI and ERP research, EEGft can isolate the brain response specifically linked to motion, separating biological motion from other processes that also occur during movement perception but are not specifically related to the movement itself. In addition, frequency tagging enables the use of a single continuous movement, which is more similar to how movements are perceived in real-life situations, instead of presenting separate movements across numerous trials.

In summary, this master thesis shows that EEG frequency tagging can be used as a novel tool to measure biological motion. The main advantage of this measurement tool is that it can measure brain responses specifically linked to presented motion. Therefore, frequency tagging will be a valuable addition to already existing instruments to measure biological motion perception.

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