EEG Frequency Tagging Objectively Measures Biological Motion Perception

Emiel Cracco[1], Danna Oomen[1], Liuba Papeo[2], Jan R. Wiersema[1]

[1]Department of Experimental Clinical and Health Psychology, Ghent University, Belgium

[2]Institut des Sciences Cognitives-Marc Jeannerod, UMR5229, Centre National de la Recherche Scientifique (CNRS) & Université Claude Bernard Lyon 1, 69675 Bron, France

Author Note

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Abstract

Various neuroimaging techniques have been developed to study the brain processes underlying biological motion perception. However, brain activity during movement perception captures a multitude of components. As a result, it is often unclear which components reflect the processing of the movement and which components reflect other, secondary processes that build on movement processing (e.g., inferring the agent's mood or identity). To address this issue, we developed and validated a new approach that objectively defines the brain response associated with biological motion perception. Specifically, we showed 30 male and female adults a point-light walker moving at a pace of 2.4 Hz and used EEG frequency tagging to measure the brain response coupled to that pace. The results revealed a reliable response at the walking frequency that was reduced by two manipulations known to disrupt biological motion perception, namely phase scrambling and inversion. Interestingly, we also identified a brain response at half the walking frequency (i.e., 1.2 Hz), corresponding to the rate at which the individual dots repeated their trajectory. In contrast to the 2.4 Hz response, the response at 1.2 Hz was increased for scrambled walkers. These results indicate that frequency tagging can be used to measure the visual processing of biological movements and can dissociate between the global (2.4 Hz) and local (1.2 Hz) processes involved in biological motion perception, at different frequencies of the brain signal.

Human movement contains a wealth of social information that observers can readily extract (Pavlova, 2012) via dedicated mechanisms for biological motion perception (e.g., Grossman et al., 2005; Pitcher & Ungerleider, 2021). To study these mechanisms, research has often used ‘point-light figures’, a type of stimuli that represent human movements as a set of moving dots placed on the major joints (Blake & Shiffrar, 2007; Johansson, 1973). Even though such point-light figures convey little more than kinematic information, early studies revealed that they nevertheless allow for a wide variety of social inferences. Indeed, not only are they easily recognized as human bodies (Johansson, 1973), they also reveal the agent’s sex (Kozlowski & Cutting, 1977), mood (Atkinson et al., 2004), and even identity (Cutting & Kozlowski, 1977).

Building on these initial findings, a number of different paradigms have been developed to study biological motion perception using point-light figures. In one of the most common paradigms, participants have to indicate whether a point-light figure is present within an array of noise made up from scrambled dots that maintain the same local movement trajectory as the original figure, but are placed in different spatial locations (Troje, 2013). Although this procedure prevents the possibility to identify biological motion from local motion features, research has shown that, under these conditions, participants are still able to detect point-light figures reasonably well (Bertenthal & Pinto, 1994; Chang & Troje, 2009), except when they are presented upside-down (Bertenthal & Pinto, 1994; Pavlova & Sokolov, 2000). This suggests that individuals use the spatial relations between the different body parts to detect biological motion (Giese & Poggio, 2003; Lange & Lappe, 2006) and hence that biological motion perception relies at least partly on configural processing (Maurer et al., 2002).

However, a downside of the behavioral approach is that participants are given the explicit task to search for biological movement. As a result, it can be difficult to disentangle

perceptual processes from attentional and other strategic processes involved in optimizing task performance (but see Thornton & Vuong, 2004, for an exception). Another measure of biological motion perception is therefore to analyze brain activity while participants passively observe moving point-light figures. Two commonly used techniques to do this are fMRI and EEG. Studies using fMRI have shown that processing biological movement involves a wide network of visual brain areas, including the extrastriate and fusiform body areas, the medial temporal cortex, and the superior temporal sulcus. In line with behavioral evidence, activity in these brain areas is reduced by manipulations that perturb the biological movement percept, such as scrambling (e.g., Engell & McCarthy, 2013; Grossman et al., 2000; Peuskens et al., 2005) and inversion (e.g., Grossman & Blake, 2001; Pavlova et al., 2017; Peuskens et al., 2005). EEG studies have instead focused mainly on the time course of event-related potentials (ERPs) elicited during biological motion perception (e.g., Chang et al., 2021; Hirai et al., 2003; White et al., 2014). Results suggest that scrambling has an effect already after 150-200 ms, whereas the effect of inversion emerges only after 400 ms (White et al., 2014). Thus, despite having similar effects, scrambling and inversion appear to operate at different stages of processing.

Although both fMRI and ERP studies have greatly advanced our understanding of biological motion perception, brain activity during movement perception typically spans multiple brain areas and several ERP components. As a result, it is not always clear which aspects of the brain response specifically reflect visual movement processing and which aspects reflect secondary processes building on movement processing (e.g., White et al., 2014), such as the extraction of social features (e.g., sex, mood, identity, …) from movement kinematics (e.g., Atkinson et al., 2004; Cutting & Kozlowski, 1977; Kozlowski & Cutting, 1977; Pavlova, 2012). One way to address this issue is to lock the brain response to a cyclical movement (e.g., walking) repeating at a fixed rate, a technique called frequency tagging (for a

review, see Norcia et al., 2015). In case of walking, this should elicit a brain response that recurs every time a footstep is completed. As a result, brain activity is effectively locked to the walking frequency and movement processing is separated from other processes that also take place during movement perception, but are not specifically coupled to the movement itself.

Hence, by eliciting cyclical brain responses coupled to the rate of movement repetition, frequency tagging can provide an objective measure of movement processing. However, despite successful applications across a wide range of visual domains, including orientation detection (e.g., Braddick et al., 1986), face perception (e.g., Liu-Shuang et al., 2014), object grouping (Adibpour et al., 2021), and even visual perspective taking (e.g., Beck et al., 2018), only few studies have used frequency tagging to study motion processing. The studies that did, further focused mainly on coherent motion perception (e.g., Aissani et al., 2011; Palomares et al., 2012), a process that is dissociable from biological motion perception (Grossman et al., 2005; Mather et al., 2016; Miller et al., 2018). As a result, it remains unknown if frequency tagging can also be used to study the processing of other people's actions.

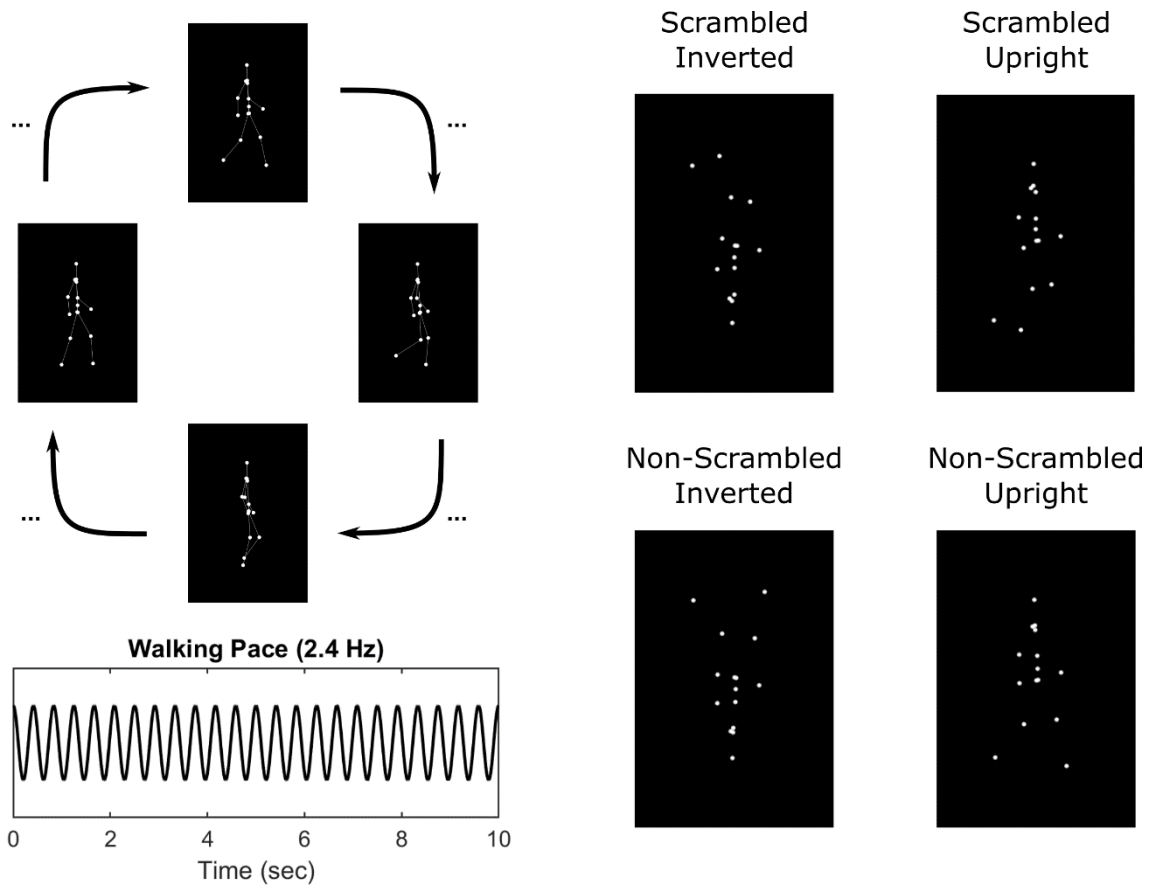
To address this issue, two studies recently combined frequency tagging with human movement stimuli. In a first study, Alp et al. (2017) measured brain responses to moving point-light figures that changed contrast at fixed frequencies. Importantly, however, these contrast changes were independent of the figures' movements. Hence, what was measured was not the processing of the movement itself, but rather the processing of visual change in a context of movement. To get a more direct measure of movement processing, Cracco et al. (2021) tagged sequences of static body postures that either did or did not form a fluent apparent movement. The results revealed dissociable responses at frequencies linked to posture and movement presentation, thereby suggesting that frequency tagging can indeed be

used to measure biological movement perception. However, by using apparent instead of actual motion, this study did not measure the visual processing of human movement kinematics, but rather its top-down reconstruction from sequences of static body postures, which is known to rely on fundamentally different processes (e.g., Giese & Poggio, 2003; Orgs et al., 2016).

In sum, despite the significant benefits associated with such an approach, it is currently unknown if frequency tagging can be used to measure the perception of human movement from kinematic information. The aim of the current study was to investigate this question by presenting a point-light figure walking at a specific frequency and measuring brain responses coupled to that frequency (Figure 1) while also manipulating two variables known to perturb biological motion perception, namely phase scrambling (e.g., Beintema et al., 2006; Troje & Westhoff, 2006) and body inversion (e.g., Bertenthal & Pinto, 1994; Pavlova et al., 2017; White et al., 2014). If frequency tagging can indeed be used to measure the visual processing of biological movement, we should see that the brain response coupled to the walker's movements is reduced when the walker is scrambled or presented upside-down.

Figure 1

Experimental Task



Note. In the task, participants saw a point-light figure walking at a fixed pace of 2.4 Hz. The walker could be presented scrambled and inverted, scrambled and upright, non-scrambled and inverted, or non-scrambled and upright. Lines between the dots were not shown in the actual experiment.

Open Science Statement

This study was preregistered (https://aspredicted.org/1P9_PNW). The stimuli, data files, analysis script, and experimental program will be made available on the OSF upon publication.

Methods

Participants

As this is the first study that uses frequency tagging to measure the processing of biological movement from kinematic patterns, we did not have strong a-priori expectations regarding the effect size. However, given that frequency tagging is known for its high stimulus-to-noise ratio (Norcia et al., 2015) and that scrambling and inversion are known to reliably disrupt biological motion perception (e.g., Bertenthal & Pinto, 1994; Grossman et al., 2000; Grossman & Blake, 2001), we reasoned that small effect sizes were unlikely. Therefore, we decided to base our sample size on a power analysis assuming 80% power for a medium effect size of $d_z = 0.50$. This revealed that we needed a sample size of $N = 33$ to detect such an effect. We further preregistered that we would collect 3 more participants if $N < 30$ following exclusions, until $N \geq 30$. Unfortunately, due to an undetected technical issue leading to bad data quality for a subset of participants (i.e., > 10% of electrodes requiring interpolation), 9 participants had to be excluded after collecting the first 33 participants. As preregistered, we therefore collected 6 (= 2 x 3) additional participants, leading to a final sample size of $N = 30$ (10 male, 20 female, $M_{age} = 23.03$, $range_{age} = 18–33$). All participants had normal or corrected-to-normal vision, had no history of neurological or psychiatric disorder, and signed an informed consent before the experiment. All procedures were approved by the ethics board of the Faculty of Psychological and Educational Sciences at Ghent University (2021/129).

Task, Stimuli, and Procedure

During EEG preparation, participants first filled out the Dutch version of the Autism Quotient questionnaire (AQ; Hoekstra et al., 2008). The AQ had good internal consistency in the current study ($\alpha = 0.78$) and was included for exploratory purposes, based on previous research suggesting anomalous processing of biological motion in autism (Federici et al., 2020; Todorova et al., 2019; Van der Hallen et al., 2019). Afterwards, during the experiment, participants were seated in a Faraday cage, approximately 80-100 cm from a 24-inch computer monitor with a 60 Hz refresh rate. The experiment was programmed in PsychoPy (Peirce et al., 2019) and consisted of 16 blocks in which participants observed a point-light walker moving at a fixed frequency of 2.4 Hz (i.e., 1 step every ~ 417 ms) for a duration of 128 steps (~ 53 sec), including a 4-step fade-in and a 4-step fade-out period (~ 2 sec each). All point-light figures were created using the online BMLStimuli tool (Troje, 2002, 2008; https://www.biomotionlab.ca/Experiments/BMLstimuli/index.html) and were shown in white against a black background at a size of ~ 250 x 520 px. The 16 blocks were divided randomly into 4 experimental conditions, constructed from combining the manipulations of phase scrambling (100% scrambled *vs.* non-scrambled) and inversion (inverted *vs.* upright). To mitigate potential habituation effects, each repetition of the same condition showed a different stimulus, namely a male or female walker, facing left or right. Furthermore, to control participants' eye gaze and their attentional focus on the screen, the central dot of the walker was colored in grey and served as a fixation cross. Participants were asked to focus on this dot and to press the spacebar every time it turned red (400 ms), which happened two to four times per block.

Preprocessing

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

Off-line processing of the EEG signal was done in Letswave 6 (www.letswave.org) according to the following steps. First, the raw data were band-pass filtered using a fourth-order Butterworth filter with 0.1 Hz and 100 Hz as cut-off values. Next, the filtered data were segmented according to the 4 experimental conditions (-2 to 54 sec), before an independent component analysis (ICA) was applied on the merged segmented data to remove ocular artefacts. Following ICA, faulty or excessively noisy electrodes were interpolated (2% on average, never more than 10%) and the data were re-referenced to the average signal across all electrodes. Next, the re-referenced epochs were cropped into epochs running from the end of the fade-in to the start of the fade-out period to ensure that epoch length was a multiple of the presentation rate. Finally, conditions were averaged and a Fast Fourier Transform was applied to transform the data to normalized (divided by N/2) amplitudes (μV) in the frequency domain.

Data Analysis

Frequency tagging elicits not only responses at the tagged frequency (F) but also at harmonics of that frequency (2F, 3F, …). Given that the brain response is spread out across

these different frequencies (Norcia et al., 2015), it is best quantified by summing the baseline-subtracted amplitudes across all relevant harmonics (Retter et al., 2021; Retter & Rossion, 2016). Therefore, as preregistered, we first determined the number of harmonics to include by (i) taking the grand-averaged amplitudes across participants, conditions, and electrodes, (ii) calculating a z-score for each frequency bin using the 10 surrounding bins on each side as baseline, excluding directly adjacent bins, and (iii) identifying the harmonics with a z-score > 2.32 (i.e., $p < .01$; for a similar approach, see Cracco et al., 2021; Retter & Rossion, 2016). This procedure identified 3 relevant harmonics: 2.4 Hz (F), 4.8 Hz (2F), and 7.2 Hz (3F). For each of these 3 harmonics, we then calculated the baseline-subtracted amplitudes for each participant, condition, and electrode using the same baseline as for the z-scores and these amplitudes were summed to quantify the brain response (Retter et al., 2021; Retter & Rossion, 2016).

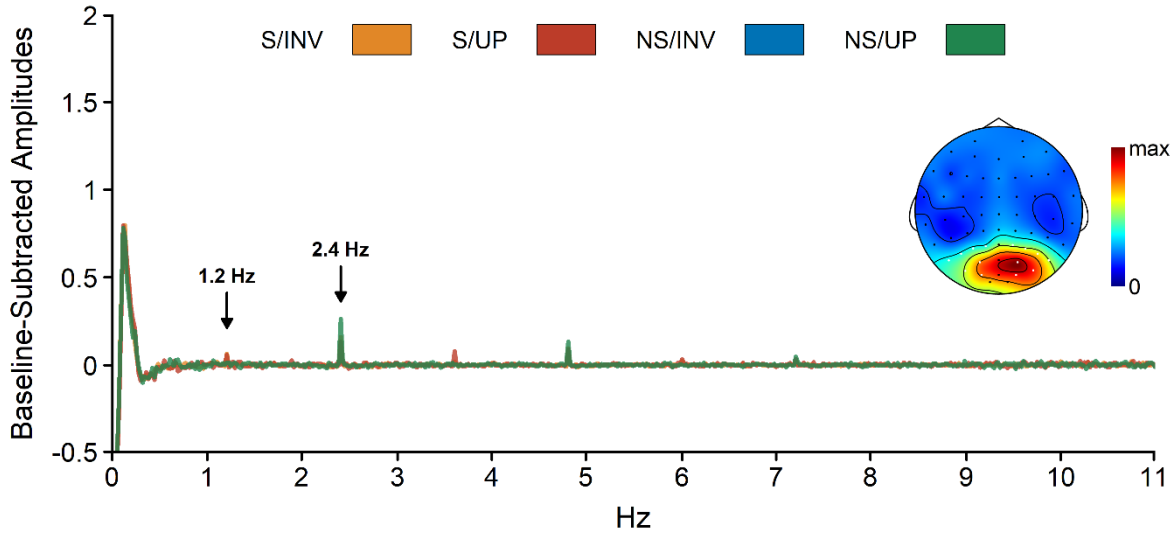
In addition to a response at 2.4 Hz, the grand-averaged amplitude spectrum also revealed a response at 1.2 Hz. This latter frequency is the frequency at which each individual dot repeated its trajectory. For example, in the non-scrambled condition, it is the frequency at which the walker took a step with the same foot. Although we had no a-priori predictions regarding this response, we nevertheless analyzed it in a preregistered secondary analysis, using the same procedure as above, but excluding those harmonics that overlapped with the 2.4 Hz response, as recommended by Retter et al. (2021). The analysis of the 1.2 Hz response revealed 2 harmonics with z > 2.32, at 3.6 Hz (F2) and 6 Hz (F3). Although not exceeding the pre-defined z-threshold, a smaller peak was also visible at 1.2 Hz (F). Given that noise is typically higher at low frequencies, it is possible that this reduced peak at 1.2 Hz did not reflect a weak response, but rather high noise. We therefore decided to also include the 1.2 Hz amplitudes in the main analysis, but observed that excluding these amplitudes did not change the results.

To determine the electrodes of interest, we used a preregistered collapsed localizer approach using the noise-subtracted amplitudes (Luck & Gaspelin, 2017). That is, we identified the relevant electrodes from the averaged topography across participants, conditions, and both responses (i.e., 1.2 Hz and 2.4 Hz). This revealed activity across all occipital, parieto-occipital, and parietal scalp locations, with a slight right-sided lateralization (Figure 2). Given that such lateralization matches previous work on biological motion perception (e.g., Grossman et al., 2000; Jokisch et al., 2005), we decided to test for right-sided dominance in the condition effects as well. More specifically, we divided the activated scalp area into two clusters comprising all O, PO, and P electrodes, except for the five electrodes on or around the midline (Oz, OI1h, OI2h, POz, and Pz), and tested for differences between these two clusters by adding laterality (left *vs.* right) as a factor to the design. Note, however, that including the five excluded electrodes did not change the results (see Supplementary Analysis).

Using the above electrodes, we conducted separate repeated measures ANOVAs for the 2.4 Hz and 1.2 Hz responses using scrambling (scrambled *vs.* non-scrambled), orientation (inverted *vs.* upright), and laterality (left *vs.* right) as within-subject factors. Furthermore, as a preregistered exploratory analysis, we also correlated the brain responses at both frequencies with the collected AQ scores. Note, however, that this latter analysis is likely underpowered.

Figure 2

Collapsed Topography and Spectrum Plot of the Baseline-Subtracted Amplitudes



Note. The collapsed topography shows the baseline-subtracted amplitudes across participants, conditions, and both brain responses. Electrodes included in the analysis are marked in white. The topography is scaled from 0 to the maximum value across all electrodes (i.e., 0.32). The spectrum plot shows the baseline-subtracted amplitudes for the included electrodes, separately for the four conditions. S = scrambled, NS = non-scrambled, INV = inverted, UP = upright.

Results

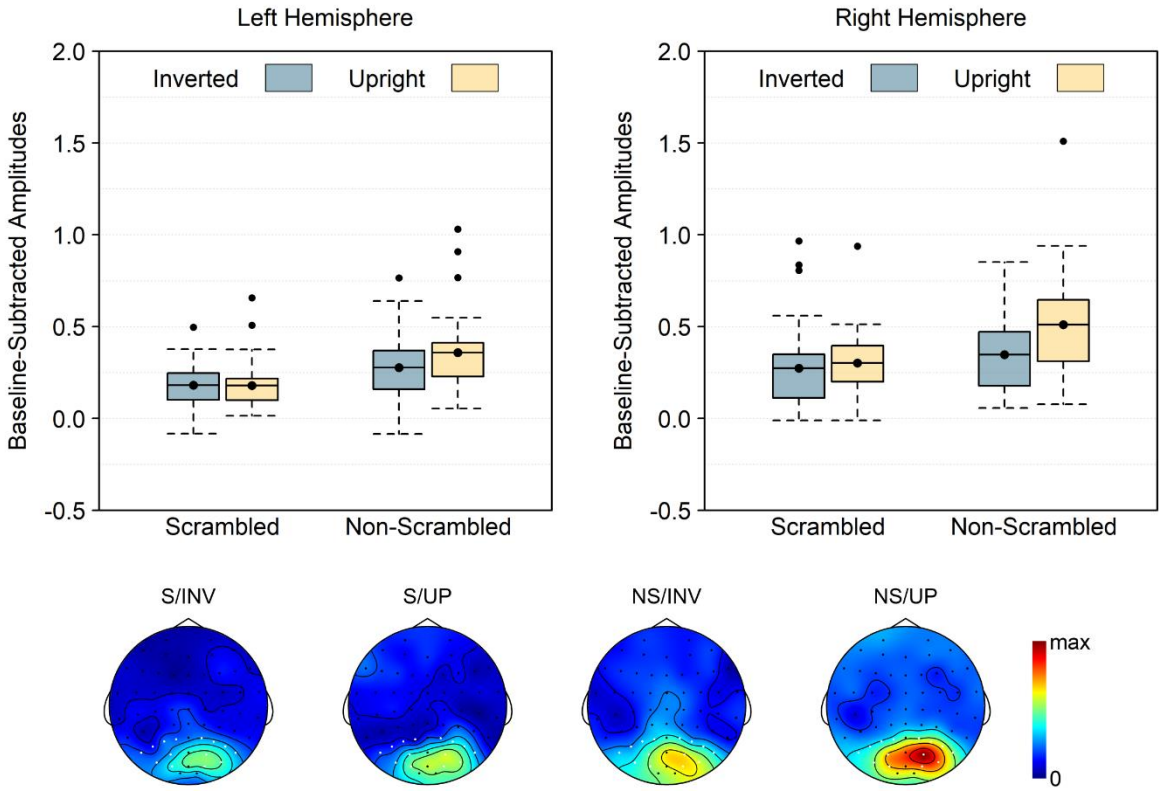
2.4 Hz Analysis

Amplitudes at 2.4 Hz (Figure 3) measure brain responses coupled to the walking cycle. Analyzing these responses revealed a main effect of scrambling, $F(1, 29) = 45.64$, $p < .001$, $d_z = 1.23$, with stronger responses in the non-scrambled than in the scrambled condition, a main effect of orientation, $F(1, 29) = 5.36$, $p = .028$, $d_z = 0.42$, with stronger responses in the upright than in the inverted condition, and a main effect of laterality, $F(1, 29) = 12.30$, $p = .002$, $d_z = 0.64$, with stronger responses across right-sided than across left-sided electrodes. In addition, we found an interaction between scrambling and orientation, $F(1, 29) = 8.50$, $p =$

.007, d_z = 0.53, indicating that there was an effect of inversion in the non-scrambled condition, $t(29) = 3.08$, $p = .005$, $d_z = 0.56$, but not in the scrambled condition, $t(29) = 0.47$, $p = .640$, $d_z = 0.08$. None of the remaining effects reached statistical significance, all $F \leq 2.04$, all $p \geq .164$. Finally, exploratory Spearman correlations revealed no significant assocations between the AQ total score and the main effect of scrambling, $r_s = 0.10$, $p = .609$, the main effect of orientation, $r_s = 0.28$, $p = .134$, or the scrambling x orientation interaction effect, $r_s = 0.17$, $p = .361$.

Figure 3

Baseline-Subtracted Amplitudes at 2.4 Hz and Harmonics



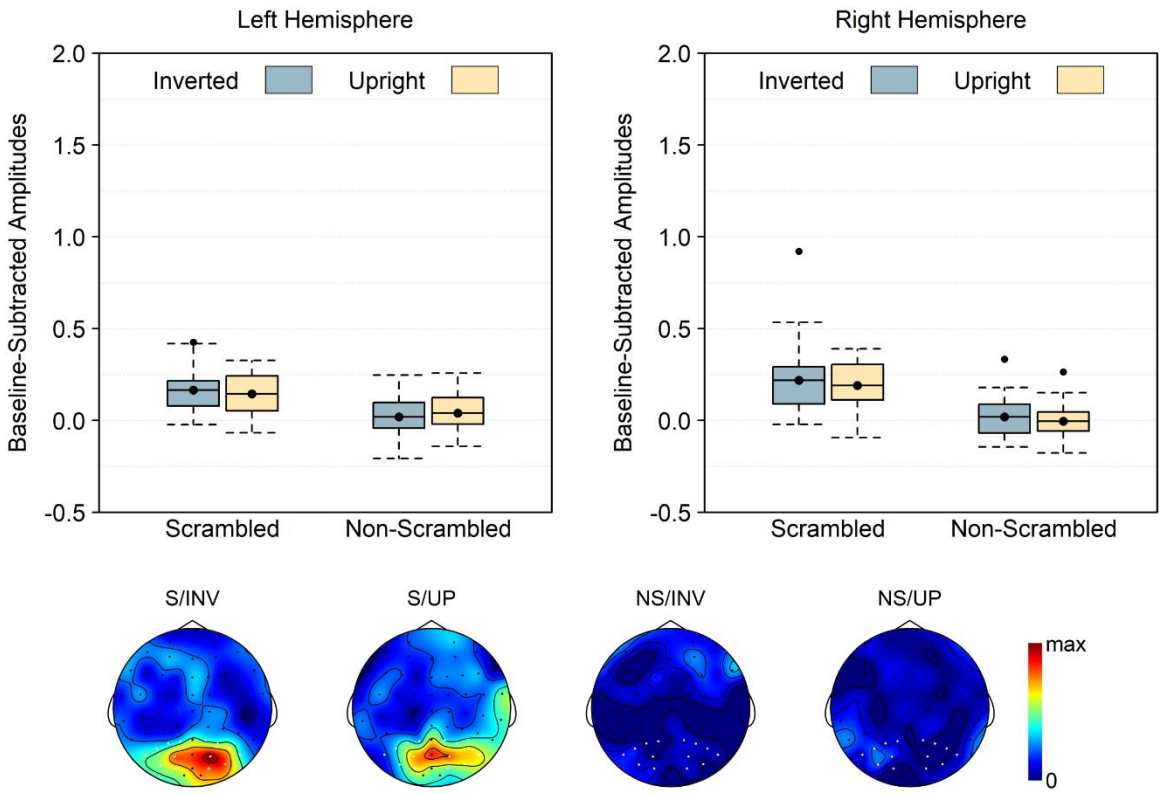
Note. Boxplots show the mean instead of median to match the statistical analysis. Note that 0 is the baseline and that values below 0 necessarily reflect noise. Topographies are plotted on a scale from 0 to the maximum across all 4 conditions (i.e., 0.74), with the included electrodes marked in white. S = scrambled, NS = non-scrambled, INV = inverted, UP = upright.

1.2 Hz Analysis

Amplitudes at 1.2 Hz (Figure 4) measure brain responses coupled to the repetition of the individual dot trajectories. Analyzing these responses revealed an inversed main effect of scrambling, $F(1, 29) = 66.26$, $p < .001$, $d_z = 1.49$, with stronger responses in the scrambled than in the non-scrambled condition. Strikingly, *t* tests comparing the 1.2 Hz response to baseline revealed that it was *only* present in the two scrambled conditions, both $t \geq 7.51$, both $p_{\text{one-tailed}} < .001$, but not in the two non-scrambled conditions, both $t \leq 1.20$, both $p_{\text{one-tailed}} \geq .120$ (see also Figure 2). In contrast to the 2.4 Hz response, the main effects of orientation, $F(1, 29) = 0.47$, $p = .499$, $d_z = 0.13$, or laterality, $F(1, 29) = 1.30$, $p = .265$, $d_z = 0.21$, were not significant, and neither was the scrambling x orientation interaction, $F(1, 29) = 0.32$, $p = .577$, $d_z = 0.10$. The laterality x scrambling interaction, however, did reach significance, $F(1, 29) = 8.90$, $p = .006$, $d_z = 0.55$, indicating that the effect of scrambling was stronger across right, $t(29) = 7.73$, $p < .001$, $d_z = 1.41$, than across left electrodes, $t(29) = 6.10$, $p < .001$, $d_z = 1.11$. None of the other effects reached significance, all $F \leq 1.04$, all $p \geq .316$. Exploratory Spearman correlations revealed no significant relation between the AQ total score and the main effect of scrambling, $r_s = 0.04$, $p = .825$, or the laterality x scrambling interaction effect, $r_s = -0.01$, $p = .965$.

Figure 4

Baseline-Subtracted Amplitudes at 1.2 Hz and Harmonics



Note. Boxplots show the mean instead of median to match the statistical analysis. Note that 0 is the baseline and that values below 0 necessarily reflect noise. Topographies are plotted on a scale from 0 to the maximum across all 4 conditions (i.e., 0.34), with the included electrodes marked in white. S = scrambled, NS = non-scrambled, INV = inverted, UP = upright.

Discussion

The results of the current study show that frequency tagging is able to capture the visual integration of local limb movements into a global, biological motion percept (Giese & Poggio, 2003). More specifically, we presented a point-light figure walking at a frequency of 2.4 Hz and measured brain responses coupled to that frequency. At the same time, we manipulated two variables known to disrupt movement processing: phase scrambling (e.g., Beintema et al., 2006; Troje & Westhoff, 2006) and inversion (e.g., Bertenthal & Pinto, 1994;

Pavlova et al., 2017; White et al., 2014). The results revealed reliable brain responses at the walking frequency that were disrupted by both scrambling and inversion. As such, these results validate frequency tagging as a tool to measure the processing of other people's actions.

Measuring biological motion perception with frequency tagging has a number of significant advantages over existing techniques. First, in contrast to fMRI and ERP studies, frequency tagging is able to isolate the brain response specifically coupled to the movement, thus providing an objective signature of biological motion perception. Second, rather than having to present separate movements across many different trials, frequency tagging can be used with a single continuous movement, more similar to movement perception in real life. Finally, frequency tagging can simultaneously measure two levels of biological motion perception. That is, biological motion can be processed in two ways: it can be processed locally, as a set of moving dots, or globally, as a moving agent (Chang & Troje, 2009b). Our results indicate that frequency tagging can disentangle them within the same stimulus. Indeed, in our task, footsteps occurred at a frequency of 2.4 Hz, but the trajectory of each individual dot repeated at a frequency of 1.2 Hz. Hence, responses at 2.4 Hz could be seen as an index of global movement processing and responses at 1.2 Hz as an index of local movement processing. In line with this interpretation, when scrambling was used to disrupt the global movement percept (Chang et al., 2018; Chang & Troje, 2009b), responses at 2.4 Hz decreased, but responses at 1.2 Hz increased. Such interactions between local and global processes are well-established in biological motion perception (e.g., Hirai et al., 2011; Wang et al., 2010) and suggest that disrupting processing at one level increases processing at the other.

The idea that the 2.4 Hz response was specific to global movement processing is further supported by the finding that it was susceptible to inversion only when the stimulus

was not scrambled. Indeed, previous research has shown that inversion perturbs not only global movement processing but also local motion processing of the feet (Chang & Troje, 2009a; Troje & Westhoff, 2006). This, in turn, causes inversion to have similar effects on scrambled and non-scrambled walkers (Troje & Westhoff, 2006). The fact that we did *not* find an inversion effect for the scrambled walker in the current study therefore indicates that the measured brain responses at 2.4 Hz were a relatively pure measure of global movement perception.

Going one step further, the pattern of results at 1.2 Hz suggests that inversion may not have influenced local motion processing at all in the current task. Indeed, whereas scrambling increased the 1.2 Hz response, inversion did not. In contrast to Troje and Westhoff (2006), this suggests that inversion had a rather specific influence on global movement perception. A likely reason for this discrepancy is that we presented the walker for an extended duration of ~ 1 minute without task instructions, whereas Troje and Westhoff (2006) presented their stimuli for no longer than a few seconds (i.e., until the response) and asked participants to identify the direction in which the figure was moving. Research has shown that such direction discrimination tasks can be solved easily based on local motion cues alone (e.g., Chang & Troje, 2009b; Troje, 2013). Given that local cues can be processed quickly in pre-cortical brain areas (Hirai & Senju, 2020), they likely dominate fast-paced direction discrimination tasks (e.g., Hirai, Saunders, et al., 2011). Showing the same stimulus for an extended period, on the other hand, may instead trigger a more global processing style. Indeed, it seems highly unlikely that participants in the current study did not realize that the inverted walker was still a walker. Hence, a plausible explanation of our findings is that both upright and inverted walkers were processed globally but that inverted walkers were processed less efficiently because they did not map neatly onto existing templates (Giese & Poggio, 2003; Lange & Lappe, 2006, 2007).

In sum, the current study shows that frequency tagging is a valid and promising measure of biological motion perception. Apart from directly and objectively measuring the online processing of continuous movements, frequency tagging will be especially useful for researchers who wish to disentangle or independently measure local and global movement processing. This is important, because both types of movement processing are known to rely on different mechanisms (e.g., Chang & Troje, 2009b). Indeed, according to a recent model, there are two mechanisms involved in biological motion perception: a 'step detection mechanism' and an 'action body evaluator' (Hirai & Senju, 2020). The first mechanism is thought to develop early in life and relies on local stimulus information such as the movement of the feet. By guiding attention to biological motion, this mechanism then gradually leads to the development of the second mechanism, involved in processing global body actions. Testing the predictions of this two-process model critically requires a method that is able to disentangle both processes. Our results suggest that frequency tagging may be able to do this without having to develop ecologically invalid, artificial stimuli that are manipulated in specific ways to contain only local or only global stimulus information (Chang et al., 2018; Chang & Troje, 2009b).

Distinguishing global from local movement processing may also be important to elucidate the biological motion perception anomalies that have been reported in autism (Federici et al., 2020; Todorova et al., 2019; Van der Hallen et al., 2019). Indeed, while some studies have found such anomalies (e.g., Nackaerts et al., 2012), other studies failed to find any difference between individuals with and without autism (e.g., Edey et al., 2019). Given that perceptual differences in autism mostly involve global processes (Happé & Frith, 2006; Van der Hallen et al., 2015, 2019), it seems likely that one reason for this inconsistency is that local and global processes are confounded in most biological motion tasks (Chang & Troje, 2009b). By teasing those two processes apart, frequency tagging could thus help to explain

exactly which aspect of biological motion perception differs between individuals with and without autism.

In sum, frequency tagging has a number of important advantages over other techniques that may help answer key questions in the field. However, it also has certain disadvantages. First, like all EEG-based methods, frequency tagging has poor spatial resolution and therefore cannot reveal the brain areas involved in processing biological motion. Second, by projecting the brain signal into the frequency domain, frequency tagging loses the temporal information provided by ERP studies. Although this temporal information could be regained by analyzing frequency tagging data not only in the frequency but also in the time domain (e.g., Retter & Rossion, 2016; Rossion et al., 2012), the lack of a baseline period in between stimuli often leads to a cyclical response. Because such cyclical responses are not separated in time, it is often difficult to determine exactly when they occur relative to stimulus onset. Instead, in such cases, only relative timing information can be obtained, by comparing the phase of the response wave across conditions (Retter & Rossion, 2016).

Furthermore, while our results clearly show that frequency tagging can be used to measure biological motion perception from kinematics, more work is still needed to determine the boundary conditions. For example, the current study used only one type of action, walking. Although walking is by far the most commonly used action in the literature and forms the basis of existing theoretical models (Giese & Poggio, 2003; Hirai & Senju, 2020; Lange & Lappe, 2006), further research will have to investigate whether frequency tagging works with other movements as well. It seems likely that it will, however, as long as the movement is cyclical (for a database of cyclical actions, see Vanrie & Verfaillie, 2004). In addition, the current study investigated only one type of scrambling, temporal scrambling, in which the phase but not the position of the different dots is scrambled. It, thus, remains an open question whether spatial scrambling has similar effects. This again seems likely,

however, given that previous research has shown, using different methods, that spatial and temporal scrambling have very similar effects on biological motion perception (e.g., Troje & Westhoff, 2006).

To conclude, we present and validate EEG frequency tagging as a new tool to measure how observers perceive biological motion from movement kinematics. This has the crucial advantage that it can measure brain responses specifically coupled to the presented movement and can dissociate local and global movement processing at different frequencies. As a result, frequency tagging will form a valuable addition to the toolbox of biological motion perception researchers.

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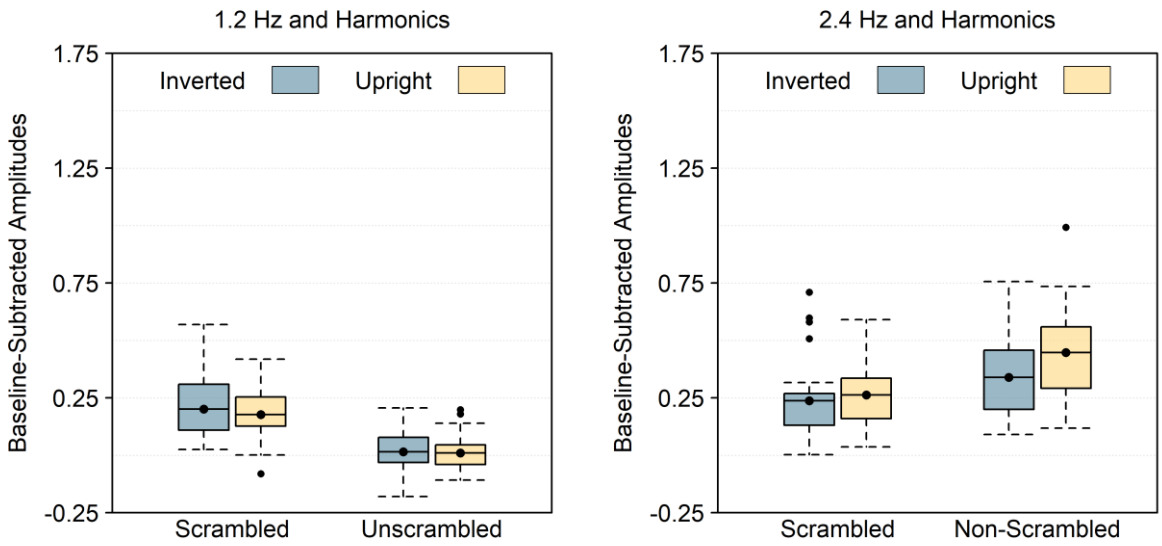
Supplementary Material:

Analysis Including Middle Posterior Electrodes

Figure S1

Baseline-Subtracted Amplitudes at 1.2 Hz and 2.4 Hz and Harmonics



Note. Boxplots show the mean instead of median to match the statistical analysis. The following electrodes are included in addition to the electrodes included in the main analysis: OI1h, OI2h, Oz, POz, and Pz. Note that 0 is the baseline and that values below 0 necessarily reflect noise.

2.4 Hz Analysis

When the five electrodes on or around the midline were included, the 2.4 Hz analysis (Figure S1) revealed a main effect of scrambling, $F(1, 29) = 47.17$, $p < .001$, $d_z = 1.25$, with stronger responses in the non-scrambled than in the scrambled condition, a main effect of orientation, $F(1, 29) = 5.22$, $p = .030$, $d_z = 0.42$, with stronger responses in the upright than in the inverted condition, and a scrambling x orientation interaction, $F(1, 29) = 5.52$, $p = .026$, $d_z = 0.43$, indicating that the orientation effect was present in the non-scrambled condition, $t(29) = 2.68$, $p = .012$, $d_z = 0.49$, but not in the scrambled condition, $t(29) = 0.95$, $p = .352$, $d_z = 0.17$.

1.2 Hz Analysis

When the five electrodes on or around the midline were included, the 2.4 Hz analysis (Figure S1) revealed a main effect of scrambling, $F(1, 29) = 69.17$, $p < .001$, $d_z = 1.52$, with stronger responses in the scrambled than in the non-scrambled condition, but no main effect of orientation, $F(1, 29) = 0.77$, $p = .389$, $d_z = 0.16$, nor a scrambling x orientation interaction, $F(1, 29) = 0.26$, $p = .618$, $d_z = 0.09$.