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Using EEG movement tagging to isolate brain responses coupled to biological movements $\stackrel{\scriptscriptstyle \star}{\times}$

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ABSTRACT

Detecting biological motion is essential for adaptive social behavior. Previous research has revealed the brain processes underlying this ability. However, brain activity during biological motion perception captures a multitude of processes. As a result, it is often unclear which processes reflect movement processing and which processes reflect secondary processes that build on movement processing. To address this issue, we developed a new approach to measure brain responses directly coupled to observed movements. 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 ('movement tagging'). The results revealed a reliable response at the walking frequency that was reduced by two manipulations known to disrupt biological motion perception: 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 completed a cycle. In contrast to the 2.4 Hz response, the response at 1.2 Hz was increased for scrambled (vs. unscrambled) walkers. These results show that frequency tagging can be used to capture the visual processing of biological movements and can dissociate between global (2.4 Hz) and local (1.2 Hz) processes involved in biological motion perception, at different frequencies of the brain signal.

The ability to recognize other living beings is key for any organism living in a social environment. One of the most important indicators of 'life' is biological motion (Troje and Westhoff, 2006). Perhaps for this reason, humans as well as other species have developed dedicated mechanisms to process such motion (Grossman et al., 2005; Pitcher and Ungerleider, 2021). These mechanisms typically make use of both shape cues (i.e., the body postures composing the movement) and motion cues (i.e., the motion patterns of the different body parts; Giese and Poggio, 2003; Hirai and Senju, 2020; Lange and Lappe, 2006), but can also detect biological movement from motion cues alone (Giese and Poggio, 2003). To study the role of motion cues, research has often used point-light figures, a type of stimuli that depicts human (or animal) movements as a set of moving dots placed on the major joints of the body (Blake and Shiffrar, 2007; Johansson, 1973). These figures convey little more than kinematic information and observers therefore have to make use of the local dot trajectories and the relationships between those

trajectories to identify the global motion pattern in the stimulus (Giese and Poggio, 2003).

Several paradigms have been developed to study this process. In one of the most common paradigms, participants have to indicate whether a point-light figure is present in an array of noise made up from scrambled dots that move in the same way as the dots in the original figure, but are scattered throughout the screen (Troje, 2013). Because the figure and noise dots have identical motion profiles, this makes it impossible to identify biological motion from local dot trajectories. Nevertheless, research has shown that point-light figures embedded in scrambled noise can be detected reasonably well (Bertenthal and Pinto, 1994; Chang and Troje, 2009). This suggests that not just local motion features but also global movement patterns contribute to biological motion perception. In support of this idea, changing the body configuration of the point-light figure by inverting it strongly disrupts the ability to discern biological agents from noise (Bertenthal and Pinto, 1994;

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Pavlova and Sokolov, 2000).

Another approach to study biological motion processing is to measure brain activity with fMRI or EEG while participants passively observe moving point-light figures. Studies using fMRI have shown that biological motion perception activates a wide network of visual brain areas, including the extrastriate and fusiform body areas, the medial temporal cortex, and the posterior superior temporal sulcus. In line with behavioral evidence, activity in these brain areas is reduced by manipulations that perturb the global movement percept, such as scrambling (e.g., Engell and McCarthy, 2013; Grossman et al., 2000; Papeo et al., 2017) or inversion (e.g., Grossman and 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). The 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 processing stages.

However, a key challenge is that brain activity recorded during biological motion perception captures not only the visual analysis of the observed movement but also other, higher-order processes that build on this analysis (e.g., White et al., 2014). For example, research has shown that observers automatically infer people's mood (e.g., Atkinson et al., 2004), sex (e.g., Kozlowski and Cutting, 1977), and identity (e.g., Cutting and Kozlowski, 1977) from the way in which they move (for a review, see Pavlova, 2012). Here, we propose to use frequency tagging to isolate those brain response associated with movement processing (Norcia et al., 2015). More specifically, we propose to measure brain responses locked to a cyclical movement (e.g., walking) repeating at a fixed rate, an approach we will refer to as 'movement tagging'. In the case of walking, this should elicit a brain response that recurs every time a footstep is completed. Importantly, because this brain response is defined by the exact timing and duration of the movement, movement processing gets separated from other processes that also take place during movement perception, but do not necessarily follow the same temporal profile.

Hence, by eliciting cyclical brain responses coupled to the rate of movement repetition, frequency tagging can isolate the brain response associated with movement processing. While a number of studies have already combined frequency tagging with biological motion stimuli (Alp et al., 2017; Burton et al., 2016; Cracco et al., 2022; Hasan et al., 2017; Zarka et al., 2014), only one study used it to tag the movement itself (Cracco et al., 2022). Cracco et al. (2022) presented repeating 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, suggesting that movement tagging can indeed be used to measure movement processing, or at least aspects of it. However, by using apparent instead of actual motion, this study did not measure the visual processing of human movement, but rather its top-down reconstruction from sequences of static body postures, which is known to rely on fundamentally different processes (e.g., Giese and Poggio, 2003; Orgs et al., 2016).

In sum, the aim of this study was to isolate the brain response associated with processing human movement from kinematic information. To this end, we developed a novel approach that separates movement processing from other processes not directly tied to the movement. That is, we presented a point-light figure walking at a fixed frequency (2.4 Hz) and measured brain responses coupled to that frequency (Fig. 1). At the same time, we also manipulated two variables known to perturb biological motion perception: phase scrambling (e.g., Beintema et al., 2006; Troje and Westhoff, 2006) and body inversion (e.g., Bertenthal and Pinto, 1994; Pavlova et al., 2017; White et al., 2014). If the measured brain response indeed captures biological movement processing, it should be reduced when the walker is scrambled or inverted.

1. Methods

1.1. Participants

As this is the first study that uses frequency tagging to measure brain responses coupled to point-light movements, we did not have strong apriori 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 and Pinto, 1994; Grossman et al., 2000; Grossman and 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 power analysis, performed using the pwr



Fig. 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. Example videos are available on the Open Science Framework (OSF; https://osf.io/xwgmy/).

package in R (Champely et al., 2020), revealed that we needed a sample size of N = 33 to detect the anticipated effect. We further preregistered that we would collect 3 more participants if N < 30 following exclusions, until $N \ge 30$. 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 × 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).

1.2. 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). Next, 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 \sim 417 ms) for a duration of 124 steps (\sim 52 s), including a 4-step fade-in and a 4-step fade-out period (~ 2 s each). The 2.4 Hz walking frequency was chosen based on visual inspection of the stimuli, using the following two criteria: (i) the walking pace should look natural, (ii) the walking frequency should not be too slow, as low-frequency responses are known to be particularly susceptible to noise

All point-light figures were created using the online BMLStimuli tool (Troje, 2002, 2008; https://www.biomotionlab.ca/Experiments/BMLsti muli/index.html) and were shown in white against a black background with a size of \sim 250 \times 520 px. The 16 blocks were randomly assigned to one of four experimental conditions, combining the manipulations of phase scrambling (100% scrambled vs. non-scrambled) and inversion (inverted vs. upright). Phase scrambling was implemented by randomly varying the phase of the different dots between 0 and 360°, causing, the trajectories of the dots to no longer be aligned in the scrambled condition. 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 to keep their attention 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. Detection accuracy was high across all conditions (i.e., 97-98%).

1.3. 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. Offline 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 s) and an independent component analysis (ICA; RUNICA algorithm, square mixing matrix) was applied to the merged segmented data. The first 10 components were inspected and those capturing eye blinks or horizontal eye movements were removed. Following ICA, faulty or excessively noisy electrodes were interpolated from the 3 closest neighbors (2% on average, never more than 10%). Fz was then reinserted and the data were re-referenced to the average signal across all electrodes. This was followed by cropping the data into epochs running from the end of the fade-in to the start of the fade-out period, thereby ensuring that epoch length was a multiple of the presentation rate. Finally, conditions were averaged and a fast Fourier transform algorithm was used to compute the discrete Fourier transform of the signal, converting it to normalized (divided by N/2, where N is the length of the data) amplitudes (μV) in the frequency domain. The bin size is defined as the inverse of the epoch length and hence was ~ 0.02 Hz (~1/48.33).

1.4. 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 and 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., 2022; Retter and Rossion, 2016). This procedure identified 3 significant 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 every 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 and 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 the individual dots repeated their trajectory. In the non-scrambled conditions, it is the frequency at which the walker took a step with the same foot. Although we had no a-priori predictions regarding the 1.2 Hz 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 (3F) and 6 Hz (5F). 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 found that excluding these amplitudes did not change the results.

To determine the electrodes of interest, we used a preregistered collapsed localizer approach using the summed baseline-subtracted amplitudes (Luck and 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). The averaged topography revealed widespread activity across all occipital, parieto-occipital, and parietal electrodes, with a slight right-sided lateralization (Fig. 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 formally include laterality in the analysis. 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 repeatedmeasures 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.

2. Results

2.1. Analysis of the 2.4 Hz response

Amplitudes at 2.4 Hz (Fig. 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 $p \ge .164$. 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 \times orientation interaction effect, $r_s = 0.17$, p= .361.

2.2. Analysis of the 1.2 Hz response

Amplitudes at 1.2 Hz (Fig. 4) measure brain responses coupled to the movement cycles of the individual dot. Analyzing these responses revealed an inverse 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 $t \ge 7.51$, both $p_{\text{one-tailed}} < 0.001$, and not in the two non-scrambled conditions, both $t \leq 1.20$, both $p_{\text{one-tailed}} \geq 0.120$ (see also Fig. 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 \times orientation interaction, F(1, 29) = 0.32, p = .577, $d_z =$ 0.10. The laterality \times 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 \times scrambling interaction effect, $r_s = -0.01$, p =.965.

3. Discussion

Separating movement processing from other processes also activated during movement perception is a key challenge in the study of biological motion perception. Here, we overcame this challenge by measuring brain responses coupled to the walking pace of a point-light figure walking at a speed of 2.4 Hz. Validating our approach, this revealed reliable brain responses at the frequency of walking, which were reduced by two manipulations well-known to disrupt movement processing: phase scrambling (e.g., Beintema et al., 2006; Troje and Westhoff, 2006) and stimulus inversion (e.g., Bertenthal and Pinto, 1994; Pavlova et al., 2017; White et al., 2014).

By tagging the movement itself, our approach goes beyond previous studies combining frequency tagging with biological motion stimuli, as these studies tagged aspects of the stimulus unrelated to the movement



Collapsed Topography and Spectrum Plot of the Baseline-Subtracted Amplitudes

Fig. 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., 0.32μ V). 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.

Baseline-Subtracted Amplitudes at 2.4 Hz and Harmonics



2.4 Hz and Harmonics

Fig. 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 µV), with the included electrodes marked in white. S: scrambled, NS:

non-scrambled, INV: inverted, UP: upright. The key effects are highlighted in the figure, with n.s.: non-significant, *: p < .05, **: p < .01.

(Alp et al., 2017; Burton et al., 2016; Hasan et al., 2017; Zarka et al., 2014). For example, Alp et al. (2017) showed four point-light dancers and changed the contrast with which these dancers were displayed in fixed cycles. This elicited brain responses at the frequency of contrast modulation, some of which were reduced when the dancers were inverted. In other words, Alp et al. (2017) found that inversion influences neural activity coupled to stimulus changes unrelated to the observed movements. Here, we show that inversion also influences neural activity coupled to the movements themselves.

Coupling brain responses to the repetition of a cyclical movement has three key advantages over existing methods. First, in contrast to previous fMRI and ERP studies, movement tagging discards all brain processes that do not exactly follow the temporal profile of the observed movement, thereby isolating the brain processes involved in the analysis of that movement. Second, it provides a signature of biological motion perception that better captures the online processing of observed movements as it occurs in real life, rather than the processing of brief and sometimes incomplete movements, artificially divided into different trials. Finally, although not predicted a-priori, movement tagging appears to naturally disentangle two ways of processing point-light figures: they can be processed globally, as a moving agent, or locally, as a set of moving dots (Chang and Troje, 2009b). In our task, global processing was captured by the brain response at 2.4 Hz, the walking pace. Indeed, supporting this view, amplitudes at 2.4 Hz were reduced when scrambling perturbed the global movement percept. However, in addition to the predicted response at 2.4 Hz, we also found a response at 1.2 Hz, coupled to the individual dot cycles. In contrast to the 2.4 Hz response, this 1.2 Hz response was not decreased but rather increased by

scrambling. Thus, our results indicate that movement tagging can disentangle global (2.4 Hz) and local (1.2 Hz) motion processing within the same stimulus and that disrupting global processing stimulates a more local processing style, consistent with previous evidence of interactions between local and global processes in biological motion perception (e.g., Hirai et al., 2011a,b; Wang et al., 2010).

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. In previous research, inversion effects have also been found for scrambled walkers, suggesting that inversion disrupts not only global but also local processing of biological motion (Chang and Troje, 2009a; Troje and Westhoff, 2006). More specifically, this research has shown that inversion not only changes the configural relationship between the dots, but also makes the motion profile of the feet inconsistent with gravitational constraints, an important cue of animacy (Chang and Troje, 2009a). Building on this finding, the fact that we did *not* find an inversion effect for the scrambled walker 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 might 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 min without task instructions, while Troje and Westhoff (2006) presented their stimuli for no longer than a few seconds and asked participants to identify the direction in

Baseline-Subtracted Amplitudes at 1.2 Hz and Harmonics



1.2 Hz and Harmonics

Fig. 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 µV), with the included electrodes marked in white. S: scrambled, NS:

non-scrambled, INV: inverted, UP: upright. The key effects are highlighted in the figure, with ***: p < .001.

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 and Troje, 2009b; Troje, 2013). Given that local cues can be processed quickly in pre-cortical brain areas (Hirai and Senju, 2020), they likely dominate fast-paced direction discrimination tasks (e. g., Hirai 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 and Poggio, 2003; Lange and Lappe, 2006, 2007).

Nevertheless, despite the above, any comparison of the responses at 1.2 and 2.4 Hz must take into account that they are harmonically related. In other words, an important question is how we can be sure that amplitudes at those two frequencies were not just two components of the same response, rather than two different responses. Two points support the latter option. First, a response at 1.2 Hz was *only* visible when the point-light walker was scrambled, making it very unlikely that the response at 2.4 Hz was merely a harmonic of the slower 1.2 Hz response in the non-scrambled conditions. Yet, it remains possible that the 2.4 Hz response was simply a 1.2 Hz harmonic in the scrambled conditions, where we did see a reliable 1.2 Hz response. However, this again seems unlikely, considering that scrambling had opposite effects at 1.2 and 2.4 Hz. Together, these findings clearly indicate that despite their harmonic relationship, amplitudes at 1.2 and 2.4 Hz tagged distinct processes (see also Cracco et al., 2022).

In sum, the movement tagging method developed here not only offers researchers a new tool to capture the online processing of biological movements, it also naturally disentangles local and global movement processing. The latter is important, because the two types of movement processing are known to rely on different mechanisms (e.g., Chang and Troje, 2009a,b). Indeed, according to a recent model, there are two main mechanisms involved in the perception of walking: a 'step detection mechanism' and an 'action body evaluator' (Hirai and Senju, 2020; see also Neri, 2009). The first mechanism is thought to develop early in life and to rely 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 the two processes. Our results show that movement tagging may be able to do so without having to develop stimuli that are manipulated to move in an unnatural way so that they contain only local or only global stimulus information (e.g., Chang et al., 2018; Chang and 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 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 and Frith, 2006; Van der Hallen et al., 2015, 2019), one reason for this inconsistency might be that local and global processes are often confounded in biological motion tasks (Chang and Troje, 2009b). By teasing those two processes apart, movement tagging could thus help explain exactly which aspects of biological motion perception differ between individuals with and without autism.

However, while our results clearly show that movement tagging can be used to measure brain responses associated with movement processing, more work is needed to determine its 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 and Poggio, 2003; Hirai and Senju, 2020; Lange and Lappe, 2006), further research will have to investigate whether movement 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 and 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. Yet this again seems likely, given that previous research has shown, using a different approach, that spatial and temporal scrambling have very similar effects on biological motion perception (e.g., Troje and Westhoff, 2006). Finally, the current study used only one presentation frequency (2.4 Hz) and it hence remains unknown to what extent similar results would be obtained with other frequencies. That said, previous research investigating face perception has shown that frequency tagging usually yields comparable responses across a wide range of frequencies (Retter and Rossion, 2016).

More research is also needed to understand the exact mechanism driving the modulation of the brain responses in our paradigm. At the most descriptive level, our results indicate that the visual system was more sensitive to regularities occurring in the stimulus at 2.4 Hz when the walker was presented upright and unscrambled but more sensitive to regularities occurring at 1.2 Hz when the walker was scrambled. At least two mechanisms could drive these modulations. First, it could be that upright, unscrambled walkers produced stronger responses at 2.4 Hz because they are more familiar and therefore more predictable. However, this seems unlikely for three reasons. First, evidence suggests that temporal predictability has only little influence on frequency-tagged responses (Quek and Rossion, 2017). Second, even if it did, predicted stimuli typically elicit a weaker, not stronger, brain response (de Lange et al., 2018). Finally, predictability cannot explain why the brain response at 2.4 Hz was strongest for the familiar (i.e., more predictable) stimulus, whereas the brain response at 1.2 Hz was strongest for the unfamiliar (i.e., less predictable) stimulus. Hence, a perhaps more plausible explanation is that different neuronal pools responded at 1.2 and 2.4 Hz. This hypothesis is consistent with the idea that responses at these two frequencies reflect two different aspects of biological motion perception (i.e., local and global perception) that are processed at different stages and involve at least partly different neural substrates (Hirai and Senju, 2020).

To conclude, the current study used frequency tagging to measure brain responses coupled to observed movements. In addition to separating movement processing from other, concomitant processing, this has the crucial advantage that it can disentangle local and global movement processing at different frequencies of the same brain signal. These results open up important new avenues for studying the visual processes that contribute to biological motion perception.

Open science statement

This study was preregistered (https://aspredicted.org/1P9_PNW). The stimuli, data files, analysis script, and experimental program are available on the OSF together with example videos (https://osf. io/xwgmy/).

Credit author statement

Emiel Cracco: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Data Curation, Writing - Original Draft, Visualization, Funding Acquisition. **Danna Oomen:** Investigation, Writing -Review & Editing. **Liuba Papeo:** Conceptualization, Writing - Review & Editing. **Jan R. Wiersema:** Conceptualization, Writing - Review & Editing, Supervision.

Data availability

The stimuli, data files, analysis script, and experimental program are available on the OSF together with example videos (https://osf. io/xwgmy/)

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2022.108395.

References

- Alp, N., Nikolaev, A.R., Wagemans, J., Kogo, N., 2017. EEG frequency tagging dissociates between neural processing of motion synchrony and human quality of multiple point-light dancers. Sci. Rep. 7, 1–9. https://doi.org/10.1038/srep44012. August 2016.
- Atkinson, A.P., Dittrich, W.H., Gemmell, A.J., Young, A.W., 2004. Emotion perception from dynamic and static body expressions in point-light and full-light displays. Perception 33 (6), 717–746. https://doi.org/10.1068/p5096.
- Beintema, J.A., Oleksiak, A., van Wezel, R.J.A., 2006. The influence of biological motion perception on structure-from-motion interpretations at different speeds. J. Vis. 6 (7), 4. https://doi.org/10.1167/6.7.4.
- Bertenthal, B.I., Pinto, J., 1994. Global processing of biological motions. Psychol. Sci. 5 (4), 221–225. https://doi.org/10.1111/j.1467-9280.1994.tb00504.x.
- Blake, R., Shiffrar, M., 2007. Perception of human motion. Annu. Rev. Psychol. 58, 47–73. https://doi.org/10.1146/annurev.psych.57.102904.190152.
- Burton, E., Wattam-Bell, J., Rubin, G.S., Atkinson, J., Braddick, O., Nardini, M., 2016. Cortical processing of global form, motion and biological motion under low light levels. Vis. Res. 121, 39–49. https://doi.org/10.1016/j.visres.2016.01.008.
- Champely, S., Ekstrom, C., Dalgaard, P., Gill, J., Weibelzahl, S., Anandkumar, A., Ford, C., Volcic, R., Rosario, H.D., 2020. Pwr: Basic Functions For Power Analysis (1.3-0. https://CRAN.R-project.org/package=pwr.
- Chang, D.H.F., Ban, H., Ikegaya, Y., Fujita, I., Troje, N.F., 2018. Cortical and subcortical responses to biological motion. Neuroimage 174, 87–96. https://doi.org/10.1016/j. neuroimage.2018.03.013.
- Chang, D.H.F., Troje, N.F., 2009a. Acceleration carries the local inversion effect in biological motion perception. J. Vis. 9 (1), 19. https://doi.org/10.1167/9.1.19, 19.
- Chang, D.H.F., Troje, N.F., 2009b. Characterizing global and local mechanisms in biological motion perception. J. Vis. 9 (5), 8. https://doi.org/10.1167/9.5.8.
- Chang, D.H.F., Troje, N.F., Ikegaya, Y., Fujita, I., Ban, H., 2021. Spatiotemporal dynamics of responses to biological motion in the human brain. Cortex 136, 124–139. https:// doi.org/10.1016/j.cortex.2020.12.015.
- Cracco, E., Lee, H., van Belle, G., Quenon, L., Haggard, P., Rossion, B., Orgs, G., 2022. EEG frequency tagging reveals the integration of form and motion cues into the perception of group movement. Cerebr. Cortex 32 (13), 2843–2857. https://doi.org/ 10.1093/cercor/bhab385.
- Cutting, J.E., Kozlowski, L.T., 1977. Recognizing friends by their walk: gait perception without familiarity cues. Bull. Psychonomic Soc. 9 (5), 353–356.
- de Lange, F.P., Heilbron, M., Kok, P., 2018. How do expectations shape perception? Trends Cognit. Sci. 22 (9), 764–779. https://doi.org/10.1016/j.tics.2018.06.002.
- Edey, R., Cook, J., Brewer, R., Bird, G., Press, C., 2019. Adults with autism spectrum disorder are sensitive to the kinematic features defining natural human motion. Autism Res. 12 (2), 284–294. https://doi.org/10.1002/aur.2052.
- Engell, A.D., McCarthy, G., 2013. Probabilistic atlases for face and biological motion perception: an analysis of their reliability and overlap. Neuroimage 74, 140–151. https://doi.org/10.1016/j.neuroimage.2013.02.025.
- Federici, A., Parma, V., Vicovaro, M., Radassao, L., Casartelli, L., Ronconi, L., 2020. Anomalous perception of biological motion in autism: a conceptual review and metaanalysis. Sci. Rep. 10 (1), 4576. https://doi.org/10.1038/s41598-020-61252-3.
- Giese, M.A., Poggio, T., 2003. Neural mechanisms for the recognition of biological movements. Nat. Rev. Neurosci. 4 (3), 179–192. https://doi.org/10.1038/nrn1057.
- Grossman, E.D., Battelli, L., Pascual-Leone, A., 2005. Repetitive TMS over posterior STS disrupts perception of biological motion. Vis. Res. 45 (22), 2847–2853. https://doi. org/10.1016/j.visres.2005.05.027.
- Grossman, E.D., Blake, R., 2001. Brain activity evoked by inverted and imagined biological motion. Vis. Res. 41 (10–11), 1475–1482. https://doi.org/10.1016/ s0042-6989(00)00317-5.

Grossman, E.D., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., Blake, R., 2000. Brain areas involved in perception of biological motion. J. Cognit. Neurosci. 12 (5), 711–720. https://doi.org/10.1162/089892900562417.

Happé, F., Frith, U., 2006. The weak coherence account: detail-focused cognitive style in autism spectrum disorders. J. Autism Dev. Disord. 36 (1), 5–25. https://doi.org/ 10.1007/s10803-005-0039-0.

Hasan, R., Srinivasan, R., Grossman, E.D., 2017. Feature-based attentional tuning during biological motion detection measured with SSVEP. J. Vis. 17 (9), 22. https://doi. org/10.1167/17.9.22.

Hirai, M., Chang, D.H.F., Saunders, D.R., Troje, N.F., 2011a. Body configuration modulates the usage of local cues to direction in biological-motion perception. Psychol. Sci. 22 (12), 1543–1549. https://doi.org/10.1177/0956797611417257.

Hirai, M., Fukushima, H., Hiraki, K., 2003. An event-related potentials study of biological motion perception in humans. Neurosci. Lett. 344 (1), 41–44. https://doi.org/ 10.1016/S0304-3940(03)00413-0.

Hirai, M., Saunders, D.R., Troje, N.F., 2011b. Allocation of attention to biological motion: local motion dominates global shape. J. Vis. 11 (3), 4. https://doi.org/ 10.1167/11.3.4, 4.

Hirai, M., Senju, A., 2020. The two-process theory of biological motion processing. Neurosci. Biobehav. Rev. 111, 114–124. https://doi.org/10.1016/j. neubiorev.2020.01.010.

Hoekstra, R.A., Bartels, M., Cath, D.C., Boomsma, D.I., 2008. Factor structure, reliability and criterion validity of the Autism-Spectrum Quotient (AQ): a study in Dutch population and patient groups. J. Autism Dev. Disord. 38 (8), 1555–1566. https:// doi.org/10.1007/s10803-008-0538-x.

Johansson, G., 1973. Visual perception of biological motion and a model for its analysis. Percept. Psychophys. 14 (2), 201–211. https://doi.org/10.3758/BF03212378.

Jokisch, D., Daum, I., Suchan, B., Troje, N., 2005. Structural encoding and recognition of biological motion: evidence from event-related potentials and source analysis. Behav. Brain Res. 157 (2), 195–204. https://doi.org/10.1016/j.bbr.2004.06.025. Kozlowski, L.T., Cutting, J.E., 1977. Recognizing the sex of a walker from a dynamic

Kozlowski, L.I., Cutting, J.E., 1977. Recognizing the sex of a walker from a dynamic point-light display. Percept. Psychophys. 21 (6), 575–580.

Lange, J., Lappe, M., 2006. A model of biological motion perception from configural form cues. J. Neurosci. 26 (11), 2894–2906. https://doi.org/10.1523/ JNEUROSCI.4915-05.2006.

Lange, J., Lappe, M., 2007. The role of spatial and temporal information in biological motion perception. Adv. Cognit. Psychol. 3 (4), 419–428. https://doi.org/10.2478/ v10053-008-0006-3.

Luck, S.J., Gaspelin, N., 2017. How to get statistically significant effects in any ERP experiment (and why you shouldn't). Psychophysiology 54 (1), 146–157. https:// doi.org/10.1111/psyp.12639.

Nackaerts, E., Wagemans, J., Helsen, W., Swinnen, S.P., Wenderoth, N., Alaerts, K., 2012. Recognizing biological motion and emotions from point-light displays in autism spectrum disorders. PLoS One 7 (9), e44473. https://doi.org/10.1371/journal. pone.0044473.

Neri, P., 2009. Wholes and subparts in visual processing of human agency. Proc. Biol. Sci. 276 (1658), 861–869. https://doi.org/10.1098/rspb.2008.1363.

Norcia, A.M., Appelbaum, L.G., Ales, J.M., Cottereau, B.R., Rossion, B., 2015. The steadystate visual evoked potential in vision research: a review. J. Vis. 15 (6), 4. https:// doi.org/10.1167/15.6.4, 4.

Orgs, G., Dovern, A., Hagura, N., Haggard, P., Fink, G.R., Weiss, P.H., 2016. Constructing visual perception of body movement with the motor cortex. Cerebr. Cortex 26 (1), 440–449. https://doi.org/10.1093/cercor/bhv262.

Papeo, L., Wurm, M.F., Oosterhof, N.N., Caramazza, A., 2017. The neural representation of human versus nonhuman bipeds and quadrupeds. Sci. Rep. 7 (1), 14040 https:// doi.org/10.1038/s41598-017-14424-7.

Pavlova, M., 2012. Biological motion processing as a hallmark of social cognition. Cerebr. Cortex 22 (5), 981–995. https://doi.org/10.1093/cercor/bhr156. Pavlova, M., Erb, M., Hagberg, G.E., Loureiro, J., Sokolov, A.N., Scheffler, K., 2017. Wrong way up": temporal and spatial dynamics of the networks for body motion processing at 9.4 T. Cerebr. Cortex 27 (11), 5318–5330. https://doi.org/10.1093/ cercor/bhx151.

Pavlova, M., Sokolov, A., 2000. Orientation specificity in biological motion perception. Percept. Psychophys. 62 (5), 889–899. https://doi.org/10.3758/BF03212075.

Peirce, J., Gray, J.R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., Lindeløv, J.K., 2019. PsychoPy2: experiments in behavior made easy. Behav. Res. Methods 51 (1), 195–203.

Peuskens, H., Vanrie, J., Verfaillie, K., Orban, G.A., 2005. Specificity of regions processing biological motion. Eur. J. Neurosci. 21 (10), 2864–2875. https://doi.org/ 10.1111/j.1460-9568.2005.04106.x.

Pitcher, D., Ungerleider, L.G., 2021. Evidence for a third visual pathway specialized for social perception. Trends Cognit. Sci. 25 (2), 100–110. https://doi.org/10.1016/j. tics.2020.11.006.

Quek, G.L., Rossion, B., 2017. Category-selective human brain processes elicited in fast periodic visual stimulation streams are immune to temporal predictability. Neuropsychologia 104, 182–200. https://doi.org/10.1016/j. neuropsychologia.2017.08.010.

Retter, T.L., Rossion, B., 2016. Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. Neuropsychologia 91, 9–28. https://doi.org/10.1016/j.neuropsychologia.2016.07.028.

Retter, T.L., Rossion, B., Schiltz, C., 2021. Harmonic amplitude summation for frequency-tagging analysis. J. Cognit. Neurosci. 33 (11), 2372–2393. https://doi. org/10.1162/jocn_a_01763.

Todorova, G.K., Hatton, R.E.M., Pollick, F.E., 2019. Biological motion perception in autism spectrum disorder: a meta-analysis. Mol. Autism. 10, 49

Troje, N.F., 2002. Decomposing biological motion: a framework for analysis and synthesis of human gait patterns. J. Vis. 2 (5), 2. https://doi.org/10.1167/2.5.2.

Troje, N.F., 2008. Retrieving information from human movement patterns. In: Understanding Events: from Perception to Action. Oxford University Press, pp. 308–334. https://doi.org/10.1093/acprofices/9780195188370.003.0014.

Troje, N.F., 2013. What is biological motion? Definition, stimuli, and paradigms. In: Social Perception: Detection and Interpretation of Animacy. MIT Press, pp. 13–36. https://doi.org/10.7551/mitpress/9780262019279.003.0002 agency, and intention.

Troje, N.F., Westhoff, C., 2006. The inversion effect in biological motion perception: evidence for a "life detector". Curr. Biol. 16 (8), 821–824. https://doi.org/10.1016/ j.cub.2006.03.022.

Van der Hallen, R., Evers, K., Brewaeys, K., Van den Noortgate, W., Wagemans, J., 2015. Global processing takes time: a meta-analysis on local–global visual processing in ASD. Psychol. Bull. 141 (3), 549–573. https://doi.org/10.1037/bul0000004.

Van der Hallen, R., Manning, C., Evers, K., Wagemans, J., 2019. Global motion perception in autism spectrum disorder: a meta-analysis. J. Autism Dev. Disord. 49 (12), 4901–4918. https://doi.org/10.1007/s10803-019-04194-8.

Vanrie, J., Verfaillie, K., 2004. Perception of biological motion: a stimulus set of human point-light actions. Behav. Res. Methods Instrum. Comput. 36 (4), 625–629. https:// doi.org/10.3758/BF03206542.

Wang, L., Zhang, K., He, S., Jiang, Y., 2010. Searching for life motion signals: visual search asymmetry in local but not global biological-motion processing. Psychol. Sci. 21 (8), 1083–1089. https://doi.org/10.1177/0956797610376072.

White, N.C., Fawcett, J.M., Newman, A.J., 2014. Electrophysiological markers of biological motion and human form recognition. Neuroimage 84, 854–867. https:// doi.org/10.1016/j.neuroimage.2013.09.026.

Zarka, D., Cevallos, C., Petieau, M., Hoellinger, T., Dan, B., Cheron, G., 2014. Neural rhythmic symphony of human walking observation: upside-down and Uncoordinated condition on cortical theta, alpha, beta and gamma oscillations. Front. Syst. Neurosci. 8. https://www.frontiersin.org/article/10.3389/fnsys .2014.00169.