BEHAVIORAL AND NEURAL INVESTIGATION ON THE EFFECTS OF PRIOR INFORMATION ON BIOLOGICAL MOTION PERCEPTION

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By

Hüseyin Orkun Elmas

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We certify that we have read this thesis and that in our opinion it is fully adequate, in scope and in quality, as a thesis for the degree of Master of Science.

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ABSTRACT

BEHAVIORAL AND NEURAL INVESTIGATION ON THE EFFECTS OF PRIOR INFORMATION ON BIOLOGICAL MOTION PERCEPTION

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The capacity to understand the actions of others, a cognitive phenomenon known as biological motion perception, is crucial for humans. Recent research demonstrates that biological motion is processed distinctively compared to the motions of inanimate objects. A dedicated brain network for processing biological motion and actions has been uncovered through fMRI studies. M/EEG studies have revealed time windows within which biological motion processing occurs. Despite these findings, a comprehensive understanding of the fundamental mechanisms driving biological motion perception, especially the effects of top-down processes, and the temporal dimension of these effects still remain unexplored. Recent evidence in visual perception suggests that prior knowledge and expectations affect visual perception; however, the generalizability of these effects to socially important stimuli, such as biological motion, is still unknown. This study aims to illuminate the effects of prior information on the behavioral and neural mechanisms of biological motion perception.

To this end, we conducted a series of behavioral experiments and an EEG experiment to investigate the effects of prior information on biological motion perception. Through our behavioral experiments, we found that prior information influences the individuation process of biological motion, albeit conditionally. Specifically, this influence is observed only when the cue carries information about the type of action in the biological motion stimuli, and the reliability of the cue is high, at 75%.

Our EEG experiment demonstrated that correct and incorrect prior information affects the temporal dimension of biological motion perception, suggesting an early effect of prior information during biological motion processing. Moreover, a comparison of the temporal generalization matrices suggested that correct

prior information accelerates biological motion perception by accelerating the formation of related representations in the brain relative to the neutral condition. Additionally, the temporal generalization analysis results illustrate a sequence in representations within brain activity: the representation of location information precedes the representation of action type of biological motion. These results suggest that computational models, developed to model the underlying mechanisms of biological motion perception, should consider the implications of predictive processes and their temporal dimension. Furthermore, these findings support the applicability of predictive models to not only low-level stimuli but also to higher-level stimuli.

Keywords: Biological motion perception, prediction, expectation, EEG, MVPA.

ÖZET

ÖN BİLGİNİN BİYOLOJİK HAREKET ALGISI ÜZERİNDEKİ ETKİLERİNİN DAVRANIŞSAL VE NÖRAL OLARAK İNCELENMESİ

Hüseyin Orkun Elmas
Nörobilimler, Yuksek Lisans
Tez Danışmanı: Burcu Ayşen Ürgen

Diğerlerinin eylemlerini anlama kapasitesi, biyolojik hareket algısı, insanlar için hayati bir öneme sahiptir. Son araştırmalar, biyolojik hareket algısının beyinde cansız nesnelerin hareketlerine kıyasla farklı bir şekilde işlendiğini göstermektedir. fMRI çalışmaları aracılığıyla, biyolojik hareket ve eylemlerin işlenmesi için özelleşmiş bir beyin ağı ortaya çıkarılmıştır. M/EEG çalışmaları, biyolojik hareketin işlendiği zaman dilimleri hakkında önemli katkılarda bulunmuştur. Fakat, bu bulgulara rağmen, biyolojik hareket algısını yönlendiren temel mekanizmaların, özellikle üstten aşağıya işlemlerin etkileri ve bu etkilerin zamansal boyutu hakkında kapsamlı bir anlayış henüz elde edilememiştir. Görsel algı üzerindeki son çalışmalar, önbilgi ve beklentilerin görsel algıyı etkilediğini öne sürmekte; ancak, bu etkilerin sosyal öneme sahip uyaranlara genelleştirilebilirliği hala bilinmemektedir. Bu çalışma, önbilginin biyolojik hareket algısının davranışsal ve nöral mekanizmaları üzerindeki etkilerini aydınlatmayı hedeflemektedir.

Bu amaçla doğrultusunda, önbilginin biyolojik hareket algısı üzerindeki etkilerini incelemek üzere bir dizi davranışsal deney ve bir EEG deneyi yürüttük. Davranışsal çalışmamız, önbilginin biyolojik hareketin algılanması sürecini etkilediğini gösterdi, fakat bu etkinin ön bilginin güvenilirliğine ve türüne bağlı oluğunu bulduk. Özellikle, önbilginin etkisinin sadece ipucunun biyolojik hareket uyarıcısındaki eylem türü hakkında bilgi taşıdığı ve ipucunun güvenilirliğinin yüksek olduğu %75 seviyesinde gözlemlendi.

EEG deneyimiz, doğru ve yanlış önbilginin biyolojik hareket algısının zaman boyutunu etkilediğini, biyolojik hareket işlemesi sırasında önbilginin erken bir zaman aralığında etkisi olduğunu göstermektedir. Ayrıca, zamansal genelleştirme

matrislerinin karşılaştırılması, doğru önceden bilinen bilginin, beyinde ilgili temsillerin oluşmasını hızlandırarak biyolojik hareket algısını hızlandırdığını öne sürmektedir. Ek olarak, zamansal genelleştirme analizi sonuçları, biyolojik hareketin beyin aktivitesindeki temsilleri arasında bir sıralama olduğunu göstermektedir: biyolojik hareketin konum bilgisinin temsili, eylem türünün temsilinden önce gelmektedir. Bu sonuçlar, biyolojik hareket algısının altında yatan mekanizmaları modellemek amacıyla geliştirilen modellerin, tahmin süreçlerini ve bu süreçlerin zamansal boyutlarını da göz önünde bulundurması gerektiğini göstermektedir. Aynı zamanda, bu bulgular tahmine dayalı modellerin yüksek seviye uyaranlara da uygulanabilirliğini desteklemektedir.

Anahtar sözcükler: Biyolojik hareket algısı, tahmin, EEG, çok değişkenli örüntü analizi.

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Chapter 1

Introduction

The ability to perceive and understand the actions of other animals is a fundamental cognitive skill for animals. This skill is pivotal in facilitating accurate and reliable social interactions and is particularly vital in inferring the intentions behind others' actions and generating appropriate responses [3]. As a result of its social and evolutionary importance, humans and other social animals have developed advanced processing mechanisms that allow for fast and robust inferences of social information from biological motion cues [4]. Consequently, the study of biological motion perception has become a major research area in cognitive neuroscience, providing valuable insights into the neural underpinnings of this specialized skill.

1.1 Biological Motion Perception

Biological motion perception (BMP) is a specialized skill that humans and other animals use to extract valuable information from the form and motion characteristics of movements of other humans and animals (mostly referred to as biological motion). Recent studies have demonstrated that biological motion perception is a highly specialized process that is distinct from the processing

of other types of motion in our environment [5]. This distinction is reflected in the brain's neural processing of biological motion, with neuroimaging studies identifying specialized regions and networks that are selective to human forms and motions. Specifically, a special network called action observation network (AON) consisting of regions in the premotor and parietal cortices and posterior superior temporal sulcus (pSTS) has been identified to be selectively responsive to biological motion [6].

Research has shown that the perception of biological motion is a highly efficient and robust process. This efficient approach is exemplified by research on BMP using point-light display (PLD) stimuli. PLD stimuli consist of only a few illuminated points placed at key locations on a moving animal body (More details are given in section 1.2). Despite the simplicity of the information presented in PLD stimuli, humans can accurately recognize biological motion, discriminate different actions and infer important social information from the motion characteristics of PLD, such as mood, sex, affect, identity or intent [7, 8, 9] even when it is embedded in noise.

1.2 Point-light Displays

PLD stimuli have become one of the most common approaches in studying biological motion perception. PLDs are essentially human or other animal figures formed by a small number of points on the major joints of the animal 1.1. PLDs are widely used in BMP research since Johanson's point-like walkers [10] because they provide a simple and controlled way of presenting biological motion information while allowing for the study of various complex actions. Initially, these PLD stimuli were created by capturing an actor or an actress performing a specific action while wearing a dark suit with light sources attached to their major joints against a dark background. With today's technological advancements, there are publicly available databases that include PLDs for different actions, actors, and actresses, which allows researchers to study BMP using a wide variety of stimuli.

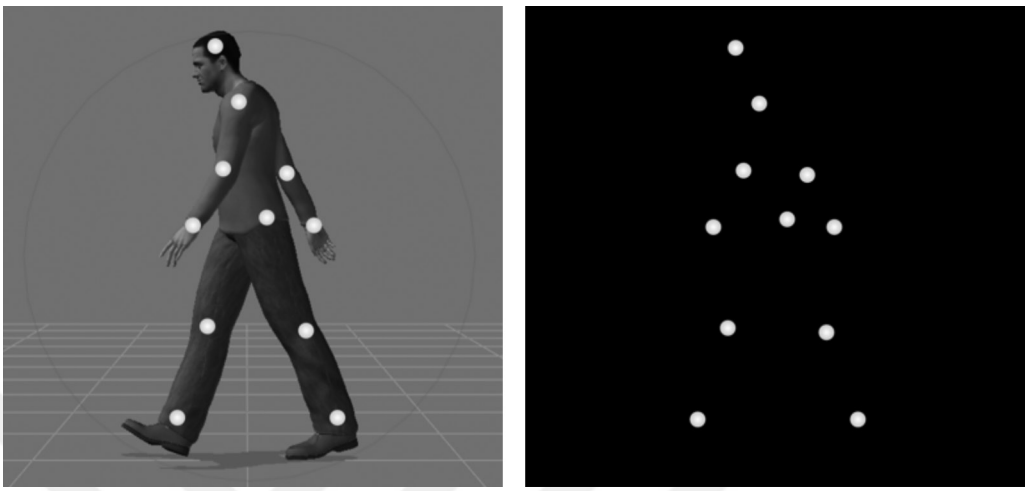

Figure 1.1: An example point light display stimulus for biological motion (Taken from [1] with permisson)

One of the key advantages of using PLDs is that they allow researchers to isolate the relevant motion and form information from other irrelevant information such as color, texture, shape, and background, and therefore decrease the number of possible confounds in the experiment [11]. Additionally, PLDs can easily be manipulated to have different motion or form characteristics which make the study of different features of BMP easier. For instance, one can scramble the point lights in spatial dimension to interrupt the form information in the PLD (Figure 1.2 B) or modify the timings of different frames to interrupt motion information. One can also make the information in PLDs vaguer by adding randomly moving noise dots (Figure 1.2 C) or modifying the contrasts of the point-lights [12]. Moreover, brain imaging studies suggest selective regions for biological motion even with PLD stimuli [13, 14, 3]. Using PET, Bondo et al. 1996 found that the posterior portion of STS was activated for coherent PLD but not activated for scrambled PLD [15]. Later studies also found evidence for selectivity for the perception of biological motion in other brain regions such as occipital and fusiform face areas (OFA and FFA), intraparietal cortex, and areas in the premotor cortex [6, 16, 17, 18]. Additionally, recent EEG experiments also shed light on the temporal aspects of biological motion perception. These studies suggest specific

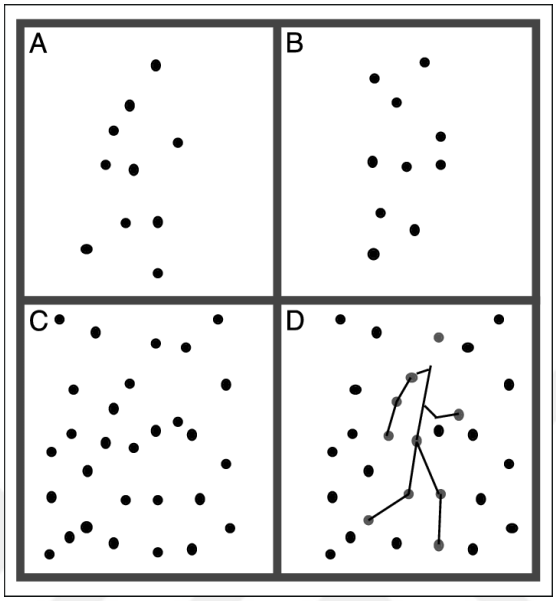

Figure 1.2: Examples of PLD biological motion, scrambled motion, and biological motion with noise. A. A point light biological motion stimulus. B. Scrambled version of the same point light stimulus. C. PLD biological motion stimulus masked in noise. D. Same figure with C, but the points belonging to the biological motion stimulus is connected with lines to reveal the biological motion (Taken from [2], with permission)

ERP components related to the perception of biological motion. A study utilizing ERP and source analysis found BM sensitive modulations between 100-200ms and 200-250ms originating from regions of motion processing and near pSTS [19]. [20] also found similar results using upright, inverted, and scrambled PLD stimuli. Specifically, they observed a negative peak at 180ms after stimulus onset, more pronounced for upright PLD, followed by a negative component around 230-360ms after stimulus for both inverted and upright stimuli originating from areas associated with visual attention and right fusiform gyrus and right superior temporal sulcus respectively. Hirai *et al.* [21] also observed a more prominent negative peak for biological motion stimuli compared to scrambled motion stimuli around 200ms and 240ms. These findings consolidate the evidence supporting the dynamic and multifaceted process of biological motion perception and suggest spatial and temporal signatures for biological motion perception.

1.3 Biological Motion Perception and Bottom-Up vs. Top-down Processing

The ease, robustness, and speed of processing biological motion in PLDs suggest BMP as an automatic, exclusively bottom-up process [10]. BMP seems to develop very early in the infancy of animals; for instance, two-day-old humans prefer to look at PLDs of biological motion rather than objects [4] and reach adult-level biological motion discrimination performance by age five[3]. Even newborn chicks with no prior visual experience still prefer biological motion [22]. In a study, Mather *et al.* found that perception of the walker was dependent on low-level visual mechanisms that operate over small spatial and temporal windows by manipulating the time intervals between each frame of a PLD walker [23]. Form and motion information in the PLDs provides plenty of evidence for recognizing biological motion; therefore, in many cases, BMP might be almost entirely driven by bottom-up processing. Models of BMP that are only bottom-up, such as Giese and Poggio's (2003), can model human performance remarkably well in many aspects [24]. The success of these models might be seen as evidence of the automatic nature of BMP. In most experimental situations, the bottom-up processing might be enough to perceive BM. However, following studies investigating the role of top-down and bottom-up processing in BMP found that in situations where the information extracted by the bottom-up processes is not enough to clarify the input, such as when the stimulus is ambiguous, degraded, distorted, or embedded in noise, top-down processes created a difference in the perception of biological motion [3]. Much like other stimuli in nature, the motions of other organisms are also almost always ambiguous; for instance, an obstacle might partly cover the creature, or other moving objects might be close to the creature making its movements more challenging to disassociate. Therefore BMP in the real world might be affected by top-down processing. In line with this intuition, research suggests that top-down processing, such as attention and expectation, affects BMP. For instance, Cavanagh *et al.* found that search for biological motion among other distractors requires attention [25]. Similarly, Thornton *et al.* show the importance of attention to detect PLDs in cases where

bottom-up processing is distorted while also showing no effect of attention in cases where bottom-up processing is allowed [26]. Parasuraman and colleagues show that sustained attention to a demanding task can decrease the performance of detection BM targets but only in visually degraded viewing conditions, [27]. Investigating the effects of attention on BM sensitive ERP components, Hirai *et al.* [28] found N330, a negative ERP component at 330ms after stimulus onset, was modulated by attention, suggesting that biological motion perception is modulated by attention.

Much like attention, expectations also play a significant role in shaping our perception of the world. Current research conceptualizes perception as the integration of bottom-up information and top-down expectations [29]. Expectation can affect perception in multiple ways, especially when the sensory information is weak or ambiguous. For instance, stimulus expectation might alter the decision-making criterion in a decision-making task [30], or expectations might sharpen the representation of the expected stimulus in the brain [31]. Moreover, there is evidence that the expectation of a feature heightens sensitivity to the stimulus with that feature [32]. There is also evidence that prior expectations might induce pre-stimulus templates [33], which help improve the tasks in which the expected feature is task-relevant. However, there is still a debate on whether the effects of expectation happen early or late in visual processing [34, 33, 29]. This might be because feature-based attention and feature-based expectation have interacting effects on the perceptual and decision-making processes, and the nature of these interactions is currently not well understood [35]. Especially regarding biological motion perception, current research makes little distinction between attention and expectation in experiment designs.

In recent years, cognitive neuroscience has made remarkable progress in uncovering the effects of expectation on the temporal dimension of visual perception by utilizing temporally precise measurements such as electroencephalography (EEG) and magnetoencephalography (MEG). An expanding body of research employing these approaches has unveiled the role of predictive processes in modulating the timing and dynamics of visual perception, allowing the brain to effectively optimize its resources and improve perceptual accuracy [36, 37, 38]. Notably, EEG

and MEG studies have demonstrated that expectation-related signals, specifically in the alpha and beta frequency bands, can impact early sensory processing and the allocation of resources [36, 39, 40, 41, 37]. Furthermore, utilizing a combination of temporally precise measurements with multivariate analysis methods such as decoding and temporal generalization, recent research was able to investigate the dynamic changes in the structure and stability of neural representations with respect to expectations [42, 31, 33, 43, 29]. Importantly, these findings highlight the role that expectations play in dynamically adjusting the brain's processing of perceptual information, shaping our visual experiences, and enhancing perceptual accuracy [35].

However, most of the research on the effects of visual expectation is done using low-level stimuli such as Gabor filters, randomly moving dots or simple lines. Using these kinds of simple stimuli can help to isolate the effects of expectation and provide insights into the predictive processing mechanism. However, they are not meaningful outside the experiment, and therefore, it is unclear whether the same expectation effects can be observed in more complex and socially important stimuli. One such study using faces and houses to investigate the effect of expectation on temporal thresholds of perceptual-decision making found that violated expectations slow down the sensory processing [44]. Another similar study found that the predictive information modulates the decision-making threshold, and thus participants make decisions faster when the predictive information is correct [45]. However, this kind of research is not common in biological motion literature.

Understanding the effect of expectation on biological motion processing would allow us to create better models of predictive processing that can generalize over more naturalistic stimuli. Additionally, using more complex stimuli allows us to investigate whether different types of information extracted from the stimulus have similar effects when expected. Biological motion is a rich stimulus, encompassing a plethora of information that can be extracted and utilized as prior knowledge. Depending on the specific nature of the extracted information, it is possible that different types of prior information, such as action category,

gender, and emotion, may be processed by distinct neural regions such as the posterior parietal cortex, anterior temporal pole, and amygdala, respectively [46, 47]. Therefore, these distinct sources of prior information may have varying impacts on biological motion perception.

The existing research on biological motion and expectation suggest an effect of expectation on the perception of biological motion. For instance, Hunt and Halper [48] found that when the point lights are replaced with complex objects, the input becomes ambiguous and naive observers cannot detect BM in the stimulus, even though the motion and form information is fully intact. However, observers that were informed about the existence of biological motion in the stimuli could reliably detect the BM. Moreover, when motion information is manipulated by increasing the blank intervals between two frames or distributing the points of the PLD to different depth planes to the point that bottom-up processing alone should not give a meaningful interpretation of the motion, observers still can perceive a coherent BM [49, 50], which suggest an effect of top-down templates informing the perception of the stimulus. In line with this work, template-matching models of biological motion perception have also been proposed [51]. These models differ from bottom-up models by incorporating a top-down process based on form information and have successfully explained BM recognition performance. Therefore, it is clear that at least in some circumstances where bottom-up information is vague, top-down information, such as expectation and attention, affects the processing of biological motion. However, currently, there is a limited amount of research exploring the impact of prior information on biological motion perception that also disentangles attention and expectation with a probabilistic cueing paradigm. As a result, it is unclear whether there is an effect of expectation on BMP and, if so, whether the type of information modulates this effect. Furthermore, there are almost no studies on the temporal dimension of the effects of expectation on biological motion perception.

To investigate the effects of prior information on biological motion. We first conducted a behavioral study, exploring prior information's impact on BM individuation performance and the factors that modulate this effect. Secondly, we conducted an EEG experiment to examine the temporal dimension of the effect

of prior information and analyze its effects on neural signals related to biological motion perception.

The impact of prior expectations on biological motion perception is a topic of interest for researchers studying perceptual processes, as it has implications for our understanding of how our brains process and interpret socially crucial visual information in the presence of contextual and environmental cues. Further investigation into this topic is necessary to provide a complete understanding of the factors that influence biological motion perception and the neural mechanisms that support this ability.

Chapter 2

Methods

2.1 Behavioral Experiments

With the behavioral experiments, we aim to investigate the effects of prior information on biological motion perception using an individuation task. We adopted a cued individuation paradigm, previously utilized in expectation and prediction literature [45, 44], which involves presenting a cue that provides information about the upcoming stimulus, to investigate how humans use prior information provided by the cues to process biological motion and extract relevant information. In this task, participants were asked to make a spatial decision based on the presented point-light display (PLD) stimuli, and we measured their reaction time and accuracy. We conducted three experiments manipulating the type of prior information. We used three different types of information, shown to be inferred from biological motion [9, 8, 7, 11]: the category of the action in Experiment 1, the mood of the actor in Experiment 2, and the gender of the actor in Experiment 3. as prior information. This prior information was employed to create an expectation for the upcoming stimuli. We manipulated the congruency of the prior information by altering the match between stimulus and cue, and we adjusted the validity of the prior information by changing the ratio of congruent trials. Adopting this paradigm and applying these manipulations, we aim to

understand how humans use prior information to process biological motion and extract relevant information. In particular, we investigate the following;

1. Does prior information about the features of PLD expedite the processing and individuation?
2. Does prior information about different types of information affect biological motion processing differently?
3. Does the validity of prior information influence its effects on biological motion perception?

In light of the literature on predictive processing and biological motion perception, we hypothesize that correct prior information about the BM increases the individuation performance by leading to faster reaction times for congruent trials. We also expect that different types of information may have varying effects on BMP. Specifically, we hypothesize that the effects of prior information on biological motion perception will be stronger for information deemed more important and relevant. Lastly, we expect the differences in the validity of the prior information to modulate its effect.

2.1.1 Participants

For the action category experiment (Experiment 1), 21 participants (14 female, with age: 22.00 ± 2.07) with ages between, for the emotion experiment, 19 participants (15 female, age: 21.15 ± 3.25) and the gender experiment 21 participants (12 female, age: 21.33 ± 2.78) were recruited for the study. To be eligible for participation, participants had to have normal or corrected to normal vision and no long-term use of neurological or psychiatric medications. The study was approved by the Human Research Ethics Committee of Bilkent University, and all participants provided written informed consent and filled out a pre-screening form prior to the experiment. Each participant attended one session per day for a total of 4 sessions, with the order of sessions randomized for each participant.

Before the first session, participants were trained on the stimuli and task. Participants were compensated with 30 TL for their participation upon completing all four sessions.

2.1.2 Stimuli and Apparatus

In the experiments, two types of visual stimuli were utilized: cues and point-light displays (PLDs). The cues were presented at the center of the screen, while the PLDs, either intact or scrambled, were displayed on the left and right sides of the screen. These stimuli were separately presented during distinct stages of a trial against a gray background. Three different types of cues 2.1 and PLDs were used across the experiments to manipulate the type of prior information. The cue stimulus was presented at the center of the screen with a size of 3.5 to 3.5 visual degrees for 2 seconds, and the PLD stimuli were presented at the left and right of the screen (with their center at seven visual degrees from the center of the screen) and with a size of 5.2 x 8.3 visual degrees. The PLD stimuli were first selected from Carnegie Mellon University's motion capture database (CMU Graphics Lab, [52]) (See figure 2.1, A). These motion capture stimuli were manipulated to fit the experimental procedure using Motion Kinematic and Kinetic Analyzer (MOKKA, 2018, [53]).

To obtain male and female walking actions, an extensive search was conducted through the Carnegie Mellon University Motion Capture Database and the Motion Capture library [54]. However,gender-specific walking stimuli suitable for the experiment were not found. Consequently, new stimuli were prepared for the gender experiment. The walking action used in the action type experiment was used to ensure compatibility between experiments as a basis for creating the new stimuli. The walking action was modified by manipulating specific point distances and positions, creating distinguishable male and female cues.

For the emotion experiment, sad and happy walking actions were selected from the same database [54]. (Figure 2.1,B)

To ensure that the PLD stimuli used in the gender and emotion experiments conveyed the necessary gender/emotion information and could be correctly classified when displayed side by side, a two-stage online survey was conducted using Qualtrics [55]. In the first stage, participants were asked to watch videos showing the prepared stimuli on a gray background and evaluate the action on a 5-point scale ranging from -2 to 2, based on gender (Female to male) or emotion (Sad to Happy). In the second stage, participants were presented with pairs of actions (happy/sad and male/female) and asked whether a particular stimulus was on the left or right side of the screen based (e.g., which side is the male walker?).

A total of 113 participants completed the survey. In the first stage, the scores given to the stimuli on a scale of -2 to 2 were: M=-0.699, SD=1.093 for Female; M=0.858, SD=1.068 for Male; M=-1.265, SD=0.876 for Sad; and M=-0.54, SD=1.536 for Happy. The dependent sample t-tests showed significant scores differences between male, female, and happy, sad stimulus pairs ($p<0.001$). To examine the results of the second stage, correct answers were coded as 1 and incorrect answers as 0, and the average accuracy of participants' responses was calculated for each question. The lowest average accuracy was 0.796 (SD=0.404), and the highest was 0.991 (SD=0.094). For each question asked in the two prior information categories, the accuracy was significantly higher than the chance level of 0.5 (all $p<0.001$).

The scrambled motion (SM) stimuli were created by randomly shuffling the starting positions of the dots in the biological motion stimuli while keeping the motion of the points fixed using BioMotion Toolbox [56]. This procedure resulted in PLDs that lacked the coherent global motion pattern of the intact BM stimuli but contained the same number of points and local motion patterns.

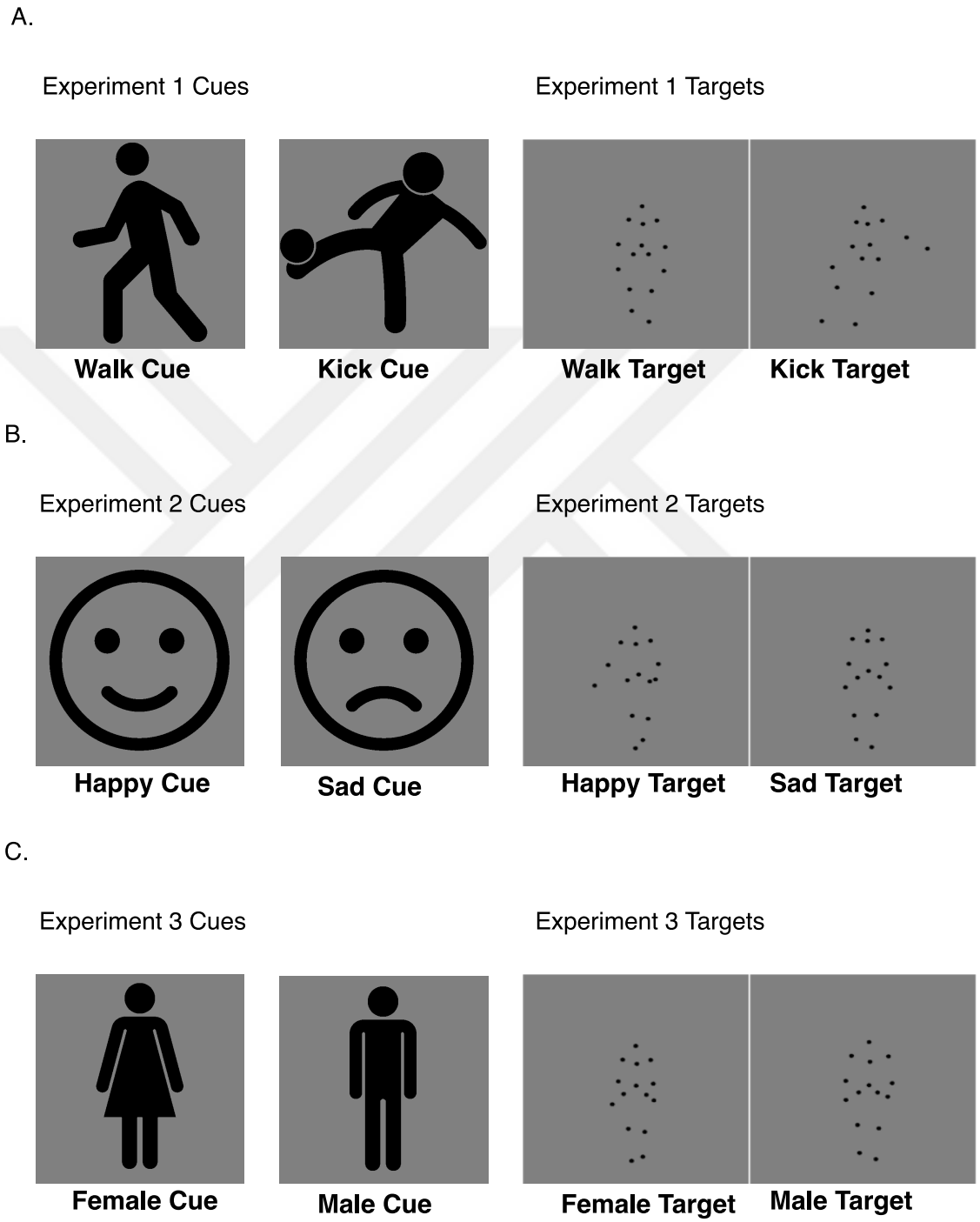

Figure 2.1: Cues and corresponding target biological motion stimuli used in the experiments. Cues are on the two left columns, and targets are on the right two columns. A. Experiment 1: Action category cues and corresponding PLD targets, B. Experiment 2: Emotion category cues and corresponding PLD targets, C. Experiment 3: Gender category cues and corresponding PLD targets

2.1.3 Experimental Design and Procedure

This section describes the experimental design used for each of the three behavioral experiments. The experiments were designed to manipulate the type of prior information provided to participants, with three types of information as a cue and PLD stimuli(action, emotion, and gender). In each experiment, we manipulated the congruency and validity of the cues. Trials can be congruent or incongruent depending on the relationship between cue and stimulus. In congruent trials, the cue provided before the PLD stimuli match the features of the stimuli, and in incongruent trials, the cue and PLD stimuli do not match (e.g., if a kick symbol is used as a cue, in congruent trials, kick PLD and scrambled PLD is displayed on the next screen, figure 2.2. Each experiment consisted of four separate sessions, where the congruent trial ratio (called "validity") of the cues was manipulated across three sessions (50%, 75%, and 100%) and a neutral session where a question mark symbol served as the cue **??**.

In each experiment, participants performed a cued individuation task adapted from [45, 44] for biological motion stimulus. Each trial started with a presentation of a cue symbol (a symbol kick or walk in experiment 1, happy or sad in experiment 2, and male or female in experiment 3, see figure 2.1) which predicted the information in the subsequent biological motion stimulus. After the cue symbol, an intact and scrambled version of a point-light biological motion stimulus were presented on the left and right sides of the screen relative to a central fixation for 1.2s (Figure 2.2). Participants were given a spatial location task in which they needed to locate the position of the biological motion stimulus and respond by pressing either the left or right arrow buttons on a keyboard. Participants could respond for the duration of the stimulus and 2s proceeding with the offset of the stimulus. For example, in experiment 1, a symbol of a kicking or walking person was presented as the cue, which predicted the action in the subsequent stimulus. Therefore, while the cues were about the features of the BM stimulus, the task was to locate the BM stimulus. This was done so that the information in the cues and the task were independent. After each trial, participants received

visual feedback on the accuracy of their response, which was displayed for 2 seconds before the subsequent trial began. To regulate the difficulty of the task and encourage the use of prior information, we embedded BM and SM stimuli in noise dots (Figure 2.2). To keep the task difficulty similar for every subject and session, we used an adaptive procedure to adjust the noise level at each trial depending on the participant's performance in previous trials (Quest) [57]. Both cue symbols and BM stimuli were balanced for each participant and presented in a randomized order for all experiments. Moreover, the target stimulus (BM) was also balanced between the right and left sides of the screen for each participant.

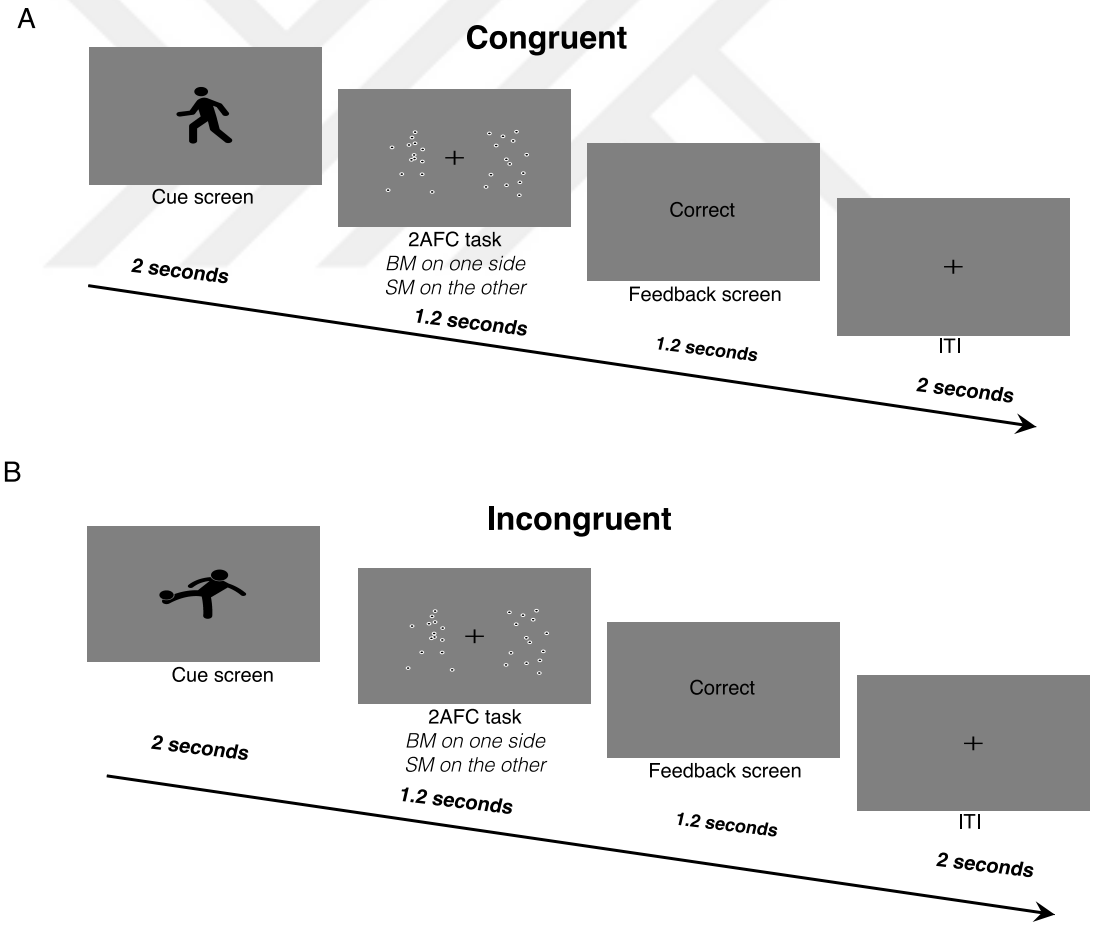

Figure 2.2: The trial structure and comparison between incongruent and congruent trials. A. A congruent trial B. An incongruent trial.

Each session consisted of 3 blocks, with a total of 288 trials. Prior to the

first session, all participants underwent a familiarization process where they were shown the biological motion stimuli and given instructions on the task. This included viewing the stimuli without noise dots, then performing the task without noise, and finally performing the task with noise for a short duration. Participants who were unable to achieve 70% accuracy during the noiseless training session were eliminated from the study. Before each subsequent session, participants were reminded of the task and stimuli by viewing the biological motion stimuli and performing practice trials with noise. Additionally, participants were informed about the validity of the cues prior to each session. During the training sessions, the cues provided were always informative and congruent.

During the sessions, participants viewed stimuli 57 cm away from a CRT screen (HP P1230, 22 inches, 85 Hz.) in the psychophysics laboratory at Aysel Sabuncu Brain Research Center. Participants were required to fixate on a central point during the task, and their heads were supported by a chin-rest that was adjustable for both height and distance from the screen.

2.1.4 Behavioral Data Analysis

In order to investigate the effects of cue congruency and validity and how these factors interact, we performed a 2 (Validity) x 2 (Congruency) repeated measures ANOVA (N= 20) on the mean reaction times of each experiment 50% and 75% conditions. As a follow-up, to investigate the differences between different validity levels, a one-way ANOVA was conducted between the mean reaction time values of Neutral, 50%, 75%, and 100% conditions for each experiment.

2.2 EEG Experiment

In the EEG experiment, we utilized a similar design with the behavioral study (see 2.1.2: Stimuli and Apparatus, and 2.1.3: Experimental Design and Procedure sections). We aim to investigate the effects of prior information effects

on the temporal dynamics of biological motion perception. Specifically, we focused on how incongruent and congruent trials compare regarding the temporal representation of the biological motion and when these differences occur.

2.2.1 Participants

Within the scope of the EEG experiment, we collected data from 20 participants. Upon examination, high artifact levels were detected in the EEG data of three participants. Therefore, the data of 17 participants were included in the analysis process. The age range of the participants was 18-29 (mean=22.2, standard deviation=2.77), with five males and 12 females. All participants were informed about the experimental procedure and had signed consent forms. After completing the EEG session, participants were paid 90 TL as compensation.

Participants took part in two sessions for the experiment. Participants were provided with information about the EEG method in the first session, and preparations for the EEG data collection process were completed. Additionally, participants were given information about the stimuli they encountered during the experiment, and a training session was administered. The main experiment was conducted in the second session, and the EEG recording was obtained.

2.2.2 Stimuli and Apparatus

The stimuli and apparatus for the EEG experiment are similar to those used in the behavioral study's action category experiment (See the section 2.1.2: Stimuli and Apparatus), with some minor differences. A neutral condition has been added to the EEG experiment to facilitate a comparison between congruent and incongruent trials. Moreover, the cue symbol in the neutral condition has been replaced with a standing human symbol (See 2.3.B) to resemble the biological cues in the other cue symbols. The experiment was conducted using an IPS monitor (The Dell Alienware AW2720HF, 27 inches, 60 Hz.).Participants viewed

the stimuli 57 cm away from the screen. Apart from these changes, the stimuli and apparatus were kept the same as in the action category experiment with a 75% validity condition.

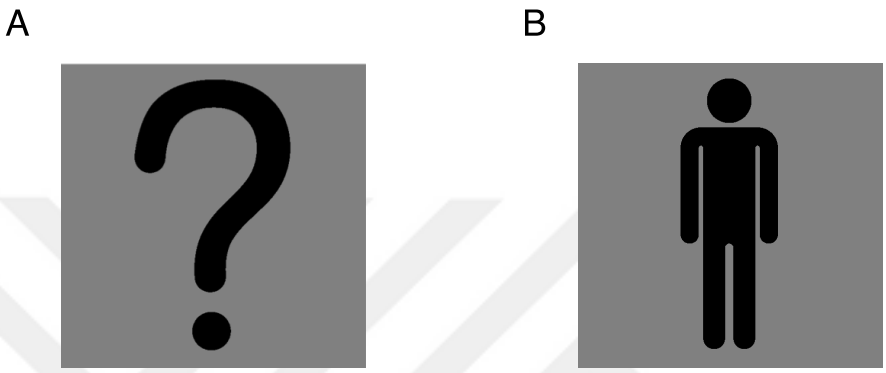

Figure 2.3: Neutral cues used in the experiments. A. A question mark symbol was used as a neutral cue in each of the behavioral experiments. B. A standing human sybmol was used as a neutral cue in the EEG experiment

2.2.3 Experimental Design and Procedure

The EEG experimental design and procedure are kept similar to the behavioral experiment's action category experiment (See the section 2.1.3: Experimental Design and Procedure), but some modifications have been made for optimization purposes. Upon examination of the reaction times in experiment 1 and the pilot runs of the EEG experiment, the maximum response time has been reduced from 2 seconds to 500 milliseconds. Moreover, the feedback screen has been removed to decrease perceptual learning and decrease the duration of a trial. Furthermore, the total number of trials has been increased to 600. The neutral condition, which was previously conducted as a separate session, has been added to the experiment with the same number of trials as the incongruent condition. Thus, the congruent, incongruent, and neutral ratios have been updated to 3:1:1.

2.2.4 EEG data collection and preprocessing

EEG was recorded using a 64-channel ActiveTwo Ag/AgCl electrodes using the BrainVision Recorder software (Brain Products, Gilching, Germany) with a 1,000Hz sampling rate. EEG electrodes were placed following the extended 10/20 system with the FCz channel as the online reference and the FPz as the ground electrode (ActiCap64 system, Brain Products GmbH, Gilching, Germany). The impedance level was kept below 15 kOhm.

The EEG data were downsampled to 500 Hz and filtered to 1-40 Hz range, thereby eliminating power line noise (which would be at 50 Hz). In the following stages, channels containing mostly corrupted data were identified using both visual inspection and statistical methods and were removed from the dataset. Removed channels were interpolated using spline interpolation in EEGLAB [58]. Subsequently, channels were re-referenced based on the average.

The re-referenced data were epoched to -2.6 to 1.5s relative to stimulus onset. These epochs were cleaned of large artifacts that were not eye artifacts using both visual and statistical inspection. Using ICA, components thought to be eye movements were removed by visual inspection. Finally, baseline correction was performed using a baseline range of -0.3 to -0.1 relative to stimulus onset.

2.2.5 Event Related Potential (ERP) Analysis

For the event-related potential (ERP) analysis, trials from the baseline-corrected data were separated according to the congruent, incongruent, and neutral conditions. Subsequently, the ERP data of all participants were combined to create the grand-average ERPs for these conditions. Statistical analyses were performed on these overall mean ERPs. For each electrode, temporal permutation cluster tests [59, 60] were applied to the EEG data. In addition, to investigate the existence of channel-time clusters, spatiotemporal permutation cluster tests were conducted on the grand-average ERP data. These analyses were performed

using MNE-Python [61].

2.2.6 Time-frequency Representation and Temporal Generalization Analysis Across Conditions

The time-frequency representation of the EEG data was calculated using Morlet wavelets, with 12 equal frequency bins created between 2 Hz and 38 Hz. The resulting data were z-scored according to the -0.3 to -0.1 reference range.

We used temporal generalization analysis across conditions [42] to investigate the temporal changes in the processes and representations that are related to the individuation of biological motion with respect to correct and incorrect prior information. Temporal generalization analyses were performed on the obtained time-frequency representation. For these analyses, a classifier consisting of PCA and LDA was created. These classifiers were trained to predict the location (left or right) and action type (kicking or walking) of the biological motion. The difference between our analysis and standard decoding analyses is that the classifier is trained and tested at each time point, and the training is done on the data collected from one experimental condition (Neutral condition in this case), while the testing is done in the other conditions (Hence the temporal generalization analysis was done across conditions). The neutral condition was selected as the training dataset because the neutral cue did not create any expectations about the biological motion stimuli; therefore, act as a baseline to compare incongruent and congruent conditions. As a result of this analysis, a matrix of scores was obtained for each participant, where the y-axis shows the training time and the x-axis shows the testing time. ROC-AUC values were calculated for scoring the classifiers. ROC-AUC is a measure used to evaluate the performance of a classification model. The ROC (Receiver Operating Characteristic) curve graphically represents the discrimination capacity of the classification model under different classification thresholds. The area under the curve (AUC) summarizes the model's discrimination power as a single numerical value, ranging between 0 and

1. The AUC value is a standard measure used to assess the classification performance of the model. The higher the AUC value, the better the classification performance of the model. Statistical results were obtained by applying permutation cluster tests [60] on the ROC-AUC in these matrices, clustering the time dimensions.

Chapter 3

Results

3.1 Behavioral Results

3.1.1 Experiment 1: Action category

Firstly, in order to investigate the effect of congruency and validity on reaction times of the participants, we selected 50% and 75% validity conditions, because only these validity conditions consisted of both congruent and incongruent trials. We run 2 (validity) x 2 (congruency) repeated measures ANOVA on these trials. We found a statistically significant main effect of congruency ($F(1,20)=5.828$, $p=0.025$, $\eta^2 = 0.226$, Table 3.1). Specifically, participants gave faster responses in congruent trials than in incongruent trials (Table: 3.2). There was no main effect of validity ($F(1,20)=1.56$, $p=0.2$). Finally, there was a marginally significant interaction effect ($F(1,20)=3.720$, $p=0.068$) (Table: 3.1, and Figure: 3.1).

Table 3.1: Results of 2x2 Anova (Congruency x Validity) on Reaction Time

Cases	Sum of Squares	df	Mean Square	F	p	η^2
Congruency	0.022	1	0.022	5.828	0.025	0.226
Residuals	0.076	20	0.004			
Validity	0.177	1	0.177	1.564	0.226	0.073
Residuals	2.267	20	0.113			
Congruency * Validity	0.006	1	0.006	3.720	0.068	0.157
Residuals	0.033	20	0.002			

Table 3.2: Post Hoc Comparisons - Congruency

		Mean Difference	SE	t	Cohen's d	p_{holm}
Congruent	Incongruent	−0.033	0.013	−2.414	−0.089	0.025

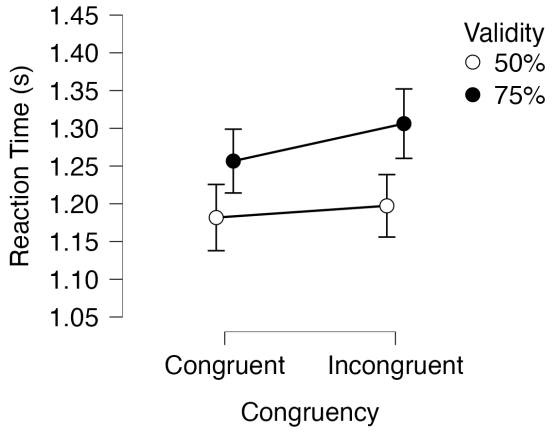

Figure 3.1: Results of 2x2 Anova (Congruency x Validity) on Reaction Time

According to the post-hoc anaylsis of the previous 2x2 ANOVA, the effect of congruency were meaningful only in 75% validity condition.(Table: 3.3).

Table 3.3: Post Hoc Comparisons - Congruency * Validity on Action Experiment Reaction Time

		Mean Difference	SE	t	p_{holm}
Congruent, A50	Incongruent, A50	−0.016	0.016	−0.966	0.970
	Congruent, A75	−0.075	0.074	−1.012	0.970
	Incongruent, A75	−0.124	0.075	−1.666	0.552
Incongruent, A50	Congruent, A75	−0.059	0.075	−0.794	0.970
	Incongruent, A75	−0.109	0.074	−1.471	0.625
Congruent, A75	Incongruent, A75	−0.050	0.016	−3.076	0.025*

When the validity levels were analyzed with respect to the reaction times of the participants, we found mean reaction times of different validity conditions as 1.261 (SD=0.193) in neutral, 1.190 (SD=0.356) in 50% validity, 1.269(SD=0.367) in 75% validity and 1.280 (SD=0.353) in 100% validity condition. We performed a One way ANOVA across validity levels on reaction times of the participants. There were no statistically significant difference between at validity levels (F(3,60)=0.796, p=0.5) (Table 3.4, Figure:3.2).

Table 3.4: Results of One way Anova (Validity) on Reactıon Time

Cases	Sum of Squares	df	Mean Square	F	p	η^2
Validity	0.105	3	0.035	0.796	0.501	0.038
Residuals	2.648	60	0.044			

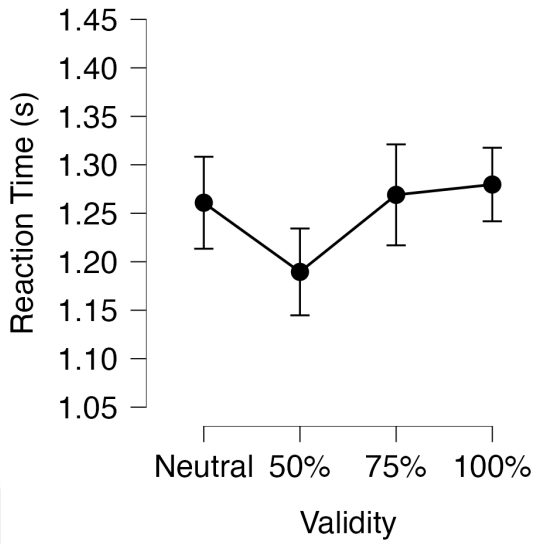

Figure 3.2: Results of One Way Anova (Validity) on Reaction Time

Overall, we found that participants responded to congruent trials faster than incongruent trials, however this effect was only significant when the cue is more likely to be congruent (in 75% condition).

3.1.2 Experiment 2, Emotion

The results of the 2 (Congruency) x 2(Validity) ANOVA on reaction times of the participants for experiment 2 show no statistically significant main effects for congruency ($F(1,18)=0.124$, $p = .728$) and validity ($F(1,18)=0.124$, $p = .728$) or an interaction effect ($F(1,18) = 0.544$, $p = 0.470$), (Table 3.5, figure 3.3).

Table 3.5: Results of 2x2 ANOVA (Congruency x Validity) on Reaction Time

Cases	Sum of Squares	df	Mean Square	F	p	η^2
Congruency	6.524×10^{-4}	1	6.524×10^{-4}	1.201	0.288	3.091×10^{-4}
Residuals	0.010	18	5.435×10^{-4}			
Validity	0.135	1	0.135	1.242	0.280	0.064
Residuals	1.953	18	0.109			
Congruency * Validity	5.141×10^{-4}	1	5.141×10^{-4}	0.790	0.386	2.436×10^{-4}
Residuals	0.012	18	6.506×10^{-4}			

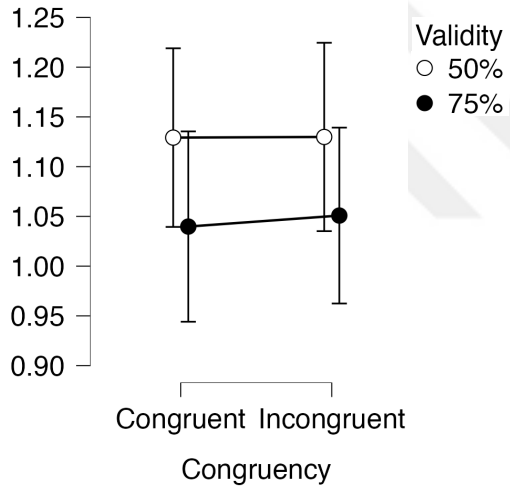

Figure 3.3: Results of the 2x2 ANOVA in Experiment 2

When reaction times of the validity levels were analyzed, we found mean reaction times of different validity conditions as 1.261 (SD=0.193) in neutral, 1.190 (SD=0.356) in 50% validity, 1.269(SD=0.367) in 75% validity and 1.280 (SD=0.353) in 100% validity condition. We then performed a One way ANOVA across validity levels. There were no statistically significant difference between at validity levels (F(3,60)=0.796, p=0.5) (Table 3.6, Figure:3.6).

Table 3.6: Within Subjects Effects

Cases	Sphericity Correction	SS	df	MS	F	p	η^2
Validity	Huynh-Feldt	0.159	2.594	0.061	1.261	0.297	0.065
Residuals	Huynh-Feldt	2.265	46.694	0.049			

Note: SS = Sum of Squares; MS = Mean Square;

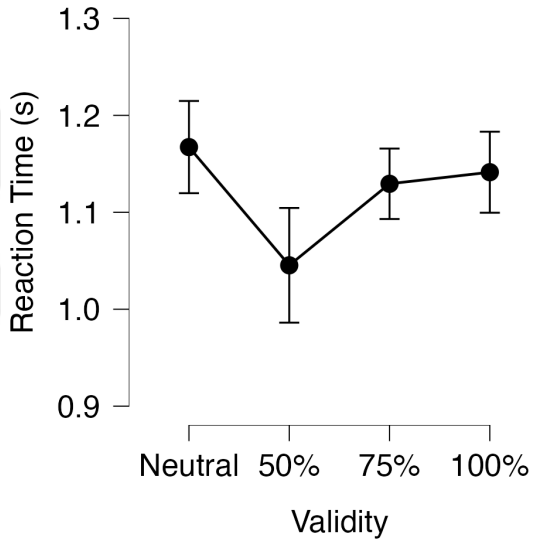

Figure 3.4: Results of the 2x2 ANOVA in Experiment 2

3.1.3 Experiment 3, Gender

The same 2 (Congruency) x 2 (Validity) ANOVA was also run on the reaction time data from experiment 3. There was no main effect of Congruency ($F(1,20)=0.124$, $p=0.728$) or main effect of validity ($F(1,20)=0.006$, $p=0.939$) or an interaction effect ($F(1,20)=0.544$, $p=0.470$).

Table 3.7: Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2
Congruency	3.757×10^{-5}	1	3.757×10^{-5}	0.124	0.728	0.006
Residuals	0.006	20	3.018×10^{-4}			
Validity	5.043×10^{-4}	1	5.043×10^{-4}	0.006	0.939	3.027×10^{-4}
Residuals	1.666	20	0.083			
Congruency * Validity	2.227×10^{-4}	1	2.227×10^{-4}	0.544	0.470	0.026
Residuals	0.008	20	4.097×10^{-4}			

Table 3.8: Descriptives for Experiment 3

Congruency	Validity	N	Mean	SD	SE	Coefficient of variation
Congruent	50%	21	1.124	0.346	0.076	0.308
	75%	21	1.132	0.299	0.065	0.264
Incongruent	50%	21	1.128	0.343	0.075	0.304
	75%	21	1.130	0.303	0.066	0.268

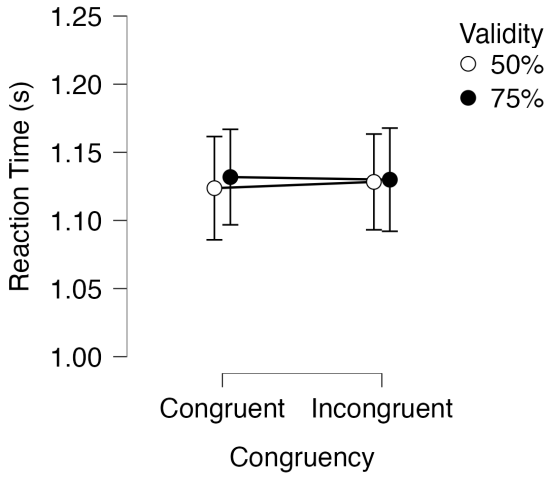

Figure 3.5: Results of the 2x2 ANOVA in Experiment 3

Following the same analysis patterns of experiments 1 and 2, We performed

a one way ANOVA across validity levels. There were no statistically significant difference between validity levels (F(3,60) = 0.473, p=0.702).

Table 3.9: Within Subjects Effects

Cases	Sum of Squares	df	Mean Square	F	p	η^2
Validity	0.046	3	0.015	0.473	0.702	0.023
Residuals	1.942	60	0.032			

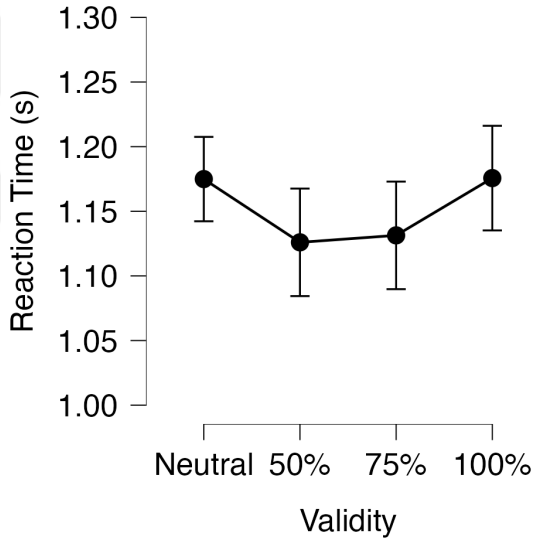

Figure 3.6: Results of the one way ANOVA in Experiment 3

Table 3.10: Descriptives of Validity Levels on Experiment 3

Validity	N	Mean	SD	SE	Coefficient of variation
Neutral	21	1.175	0.381	0.083	0.324
50%	21	1.126	0.344	0.075	0.306
75%	21	1.131	0.300	0.065	0.265
100%	21	1.176	0.402	0.088	0.342

3.2 EEG Results

3.2.1 Event-Related Potentials (ERPs)

Event-related potentials were used to investigate differences between the grand average ERPs of neutral, congruent, and incongruent conditions. The statistical test results did not reveal any significant differences between the ERPs of neutral, congruent, and incongruent trials ($p>0.05$). Similarly, the spatiotemporal clustering tests also did not find any statistically significant clusters (all clusters $p>0.05$). Below are figures illustrating the results of this analysis.

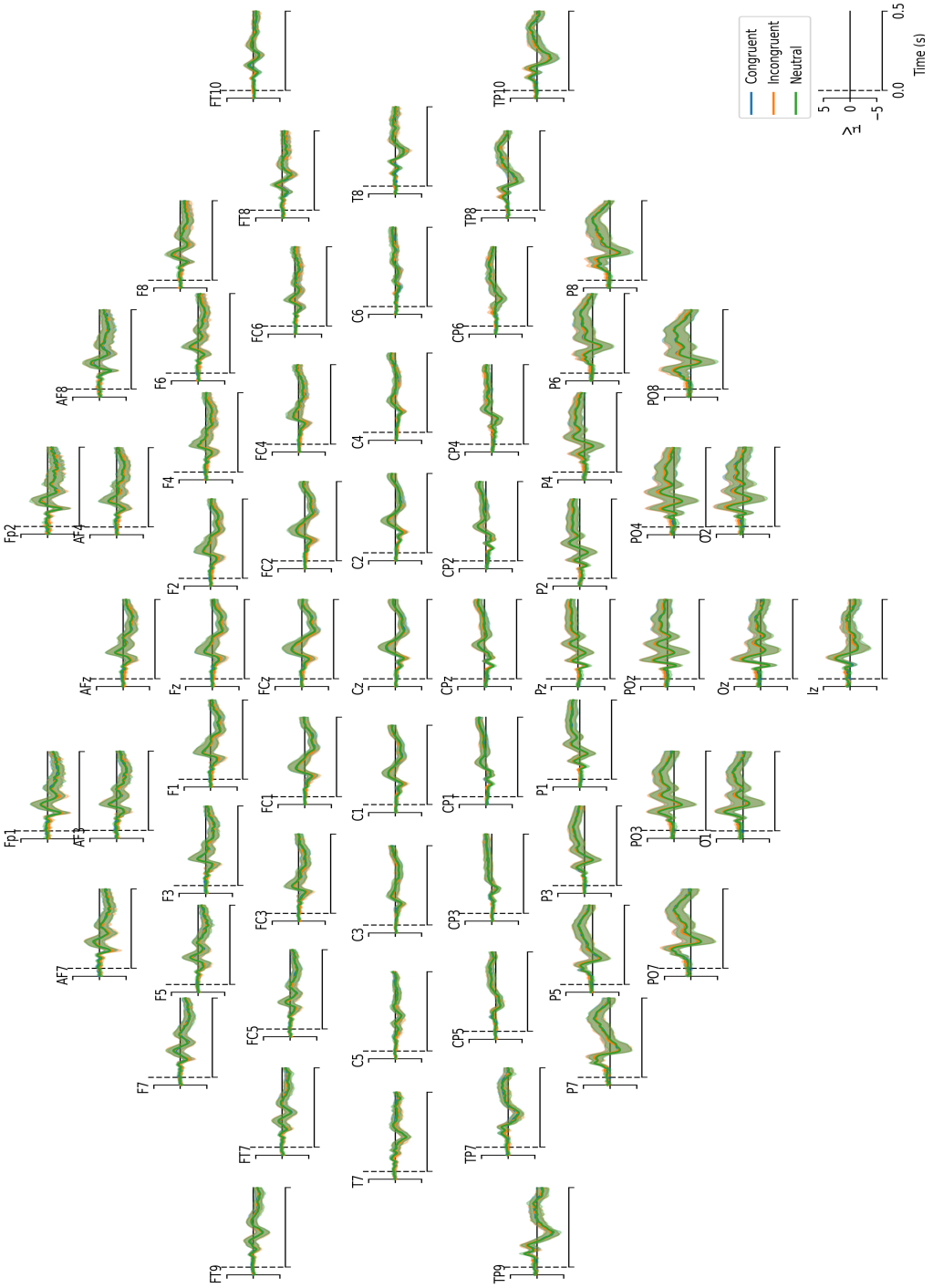

Figure 3.7: Event-related potentials across all electrodes. Neutral (green), Congruent (blue), and Incongruent (orange).

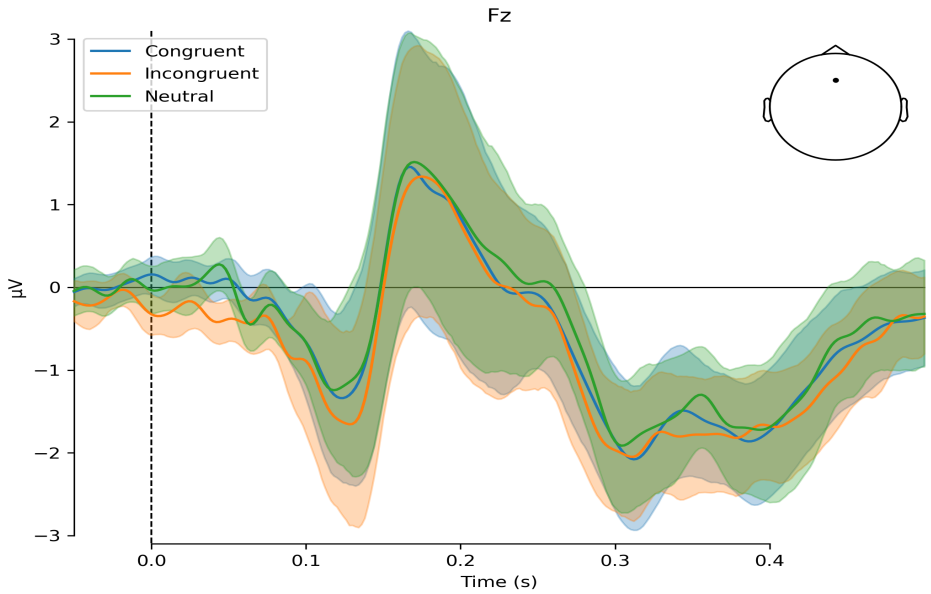

Figure 3.8: Event-related potentials at the Fz electrode. Neutral (green), Congruent (blue), and Incongruent (orange).

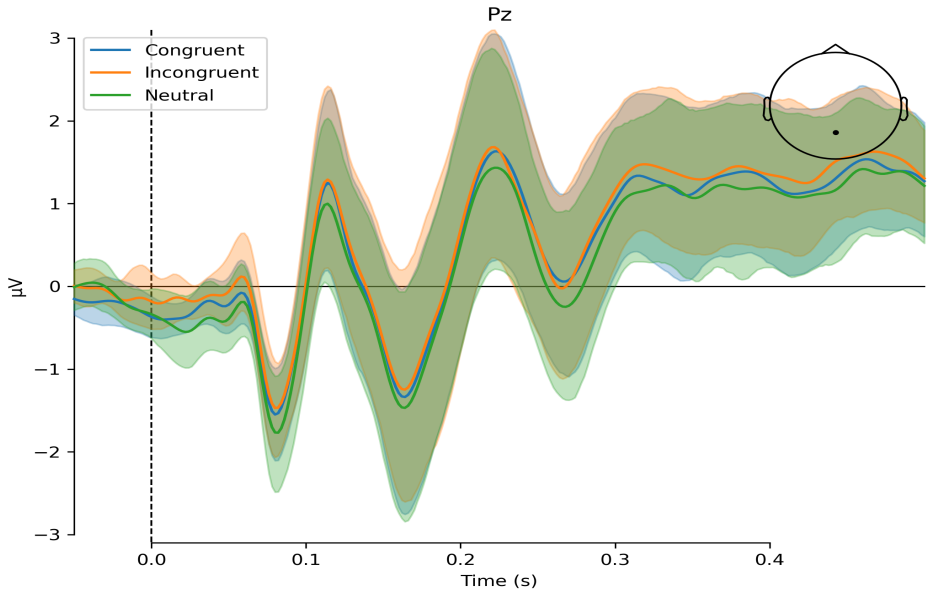

Figure 3.9: Event-related potentials at the Pz electrode. Neutral (green), Congruent (blue), and Incongruent (orange).

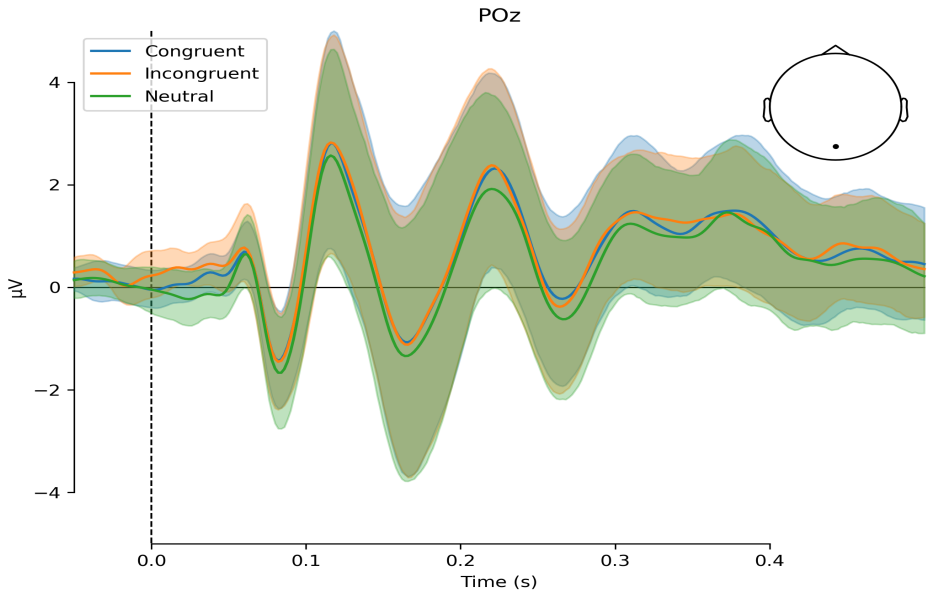

Figure 3.10: Event-related potentials at the POz electrode. Neutral (green), Congruent (blue), and Incongruent (orange).

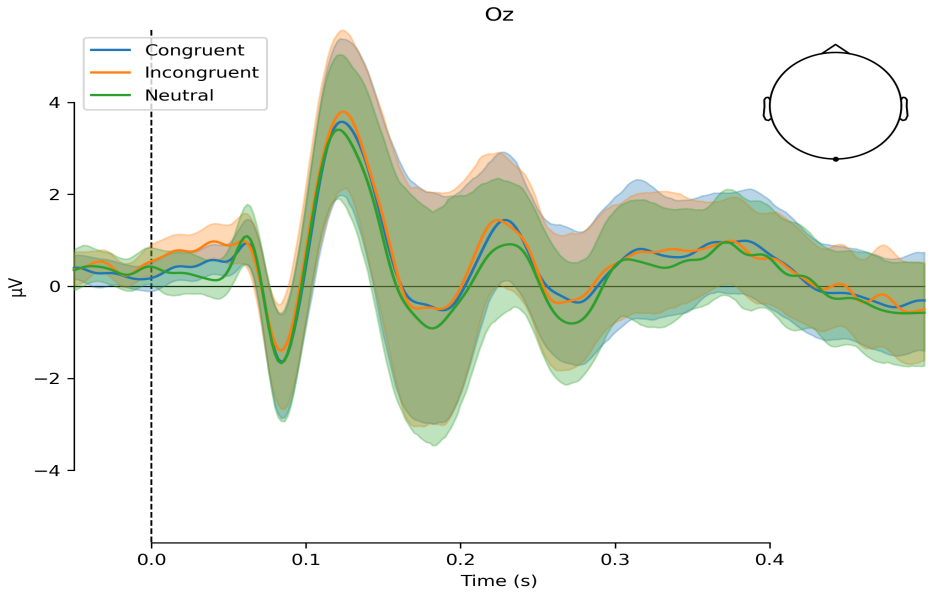

Figure 3.11: Event-related potentials at the Oz electrode. Neutral (green), Congruent (blue), and Incongruent (orange).

As can be seen in the figures above, the statistics performed on the ERP data did not reveal any statistically significant differences between neutral, congruent, and incongruent trial conditions for any electrode or electrode group .

3.2.2 Time-Frequency Representation and Temporal Generalization Across Conditions

Since the ERP analysis did not find any differences between the experimental conditions, Time frequency analysis was performed on the EEG data. Multivariate pattern analysis was used in case traditional univariate statistical analyses were insufficient in detecting differences between conditions. The temporal generalization analysis aimed to find the signatures of both the location of the biological motion and the type of biological motion in the EEG time-frequency representation.

3.2.2.1 Temporal Generalization Analysis Predicting the Type of Biological Motion in Congruent and Incongruent Trials, and trained in Neutral Trials

In this analysis, a classifier model was trained on the EEG data from neutral trials at each time point and tested on the EEG data of congruent and incongruent trials. The primary distinction used was the classification target, and type of biological motion (kicking vs. walking) in this analysis. The obtained ROC-AUC values are visualized as a heatmap (Figure 3.12, shows the temporal generalization matrix obtained from congruent trials, and figure 3.14 shows the matrix obtained from incongruent trials).

Subsequently, temporal clustering test was used to determine the intervals at which the obtained temporal generalization matrices were significantly different from the chance level (0.5 for binary classification). 3.14 shows the statistically significant ($p<0.05$) time intervals in 3.12. The gray areas indicate time intervals

that are not statistically significant.

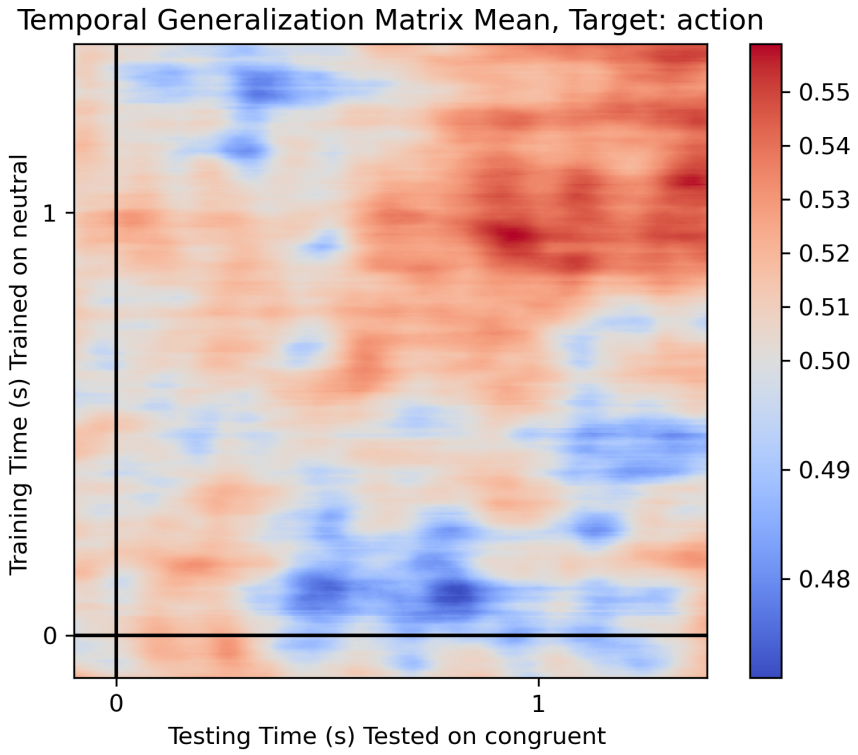

Figure 3.12: The temporal generalization analysis predicting the type of biological motion in Congruent trials. (The color bar indicates ROC-AUC scores).

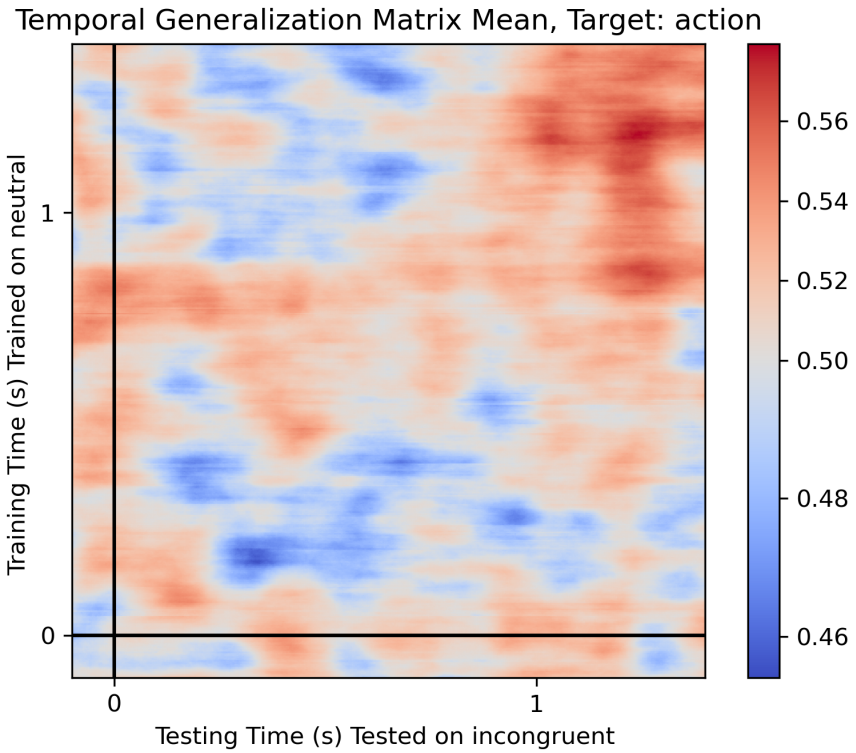

Figure 3.13: The temporal generalization analysis, predicting the type of biological motion in Incongruent trials. (The color bar indicates ROC-AUC scores).

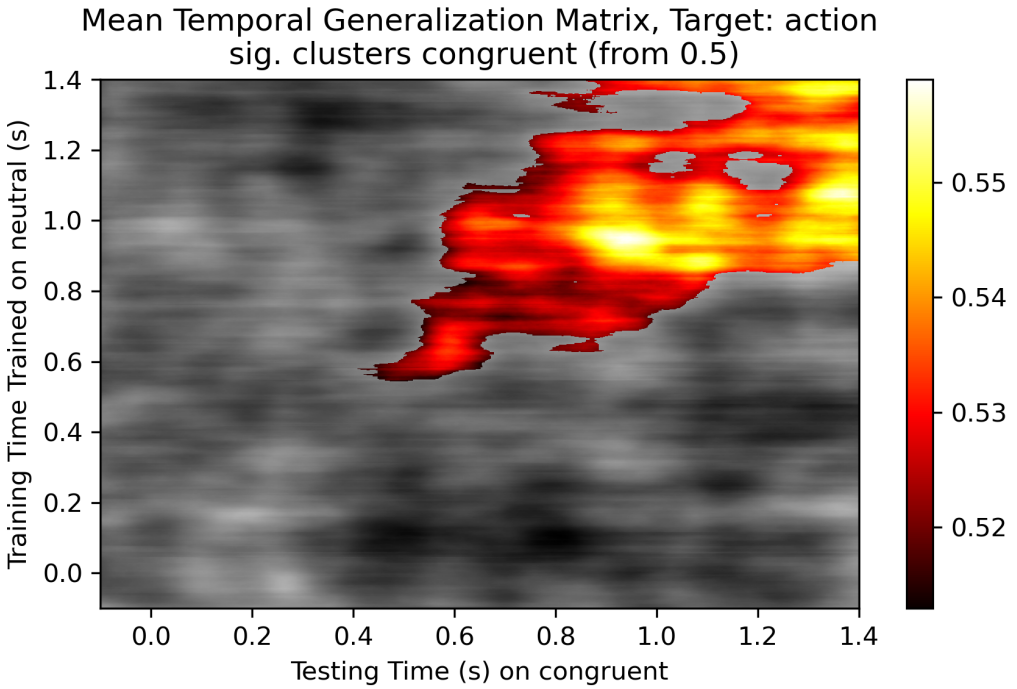

Figure 3.14: Statistical significance of the temporal generalization analysis predicting the type of biological motion in Congruent and Incongruent trials (The color bar represents the roc-auc scores, shows the statistically significant ($p<0.05$) clusters. The gray areas indicate time intervals that are not statistically significant).

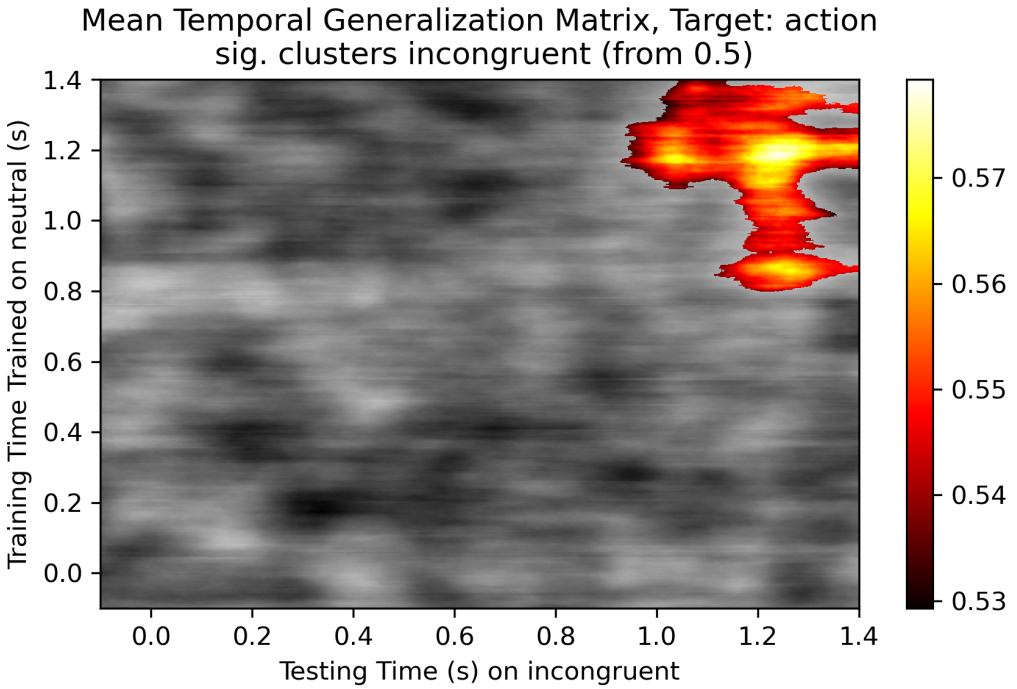

Figure 3.15: Statistical significance of the temporal generalization analysis predicting the type of biological motion in Incongruent trials (The color bar represents the roc-auc scores, shows the statistically significant ($p<0.05$) clusters. The gray areas indicate time intervals that are not statistically significant).

Comparing the temporal generalization matrices for congruent and incongruent trials in figure 3.12 and figure 3.13 and their significance from chance levels (figure 3.14 and figure 3.15), it can be observed that the representation of the type of biological motion in the brain occurs earlier in congruent trials than in incongruent trials (0.4 s vs. 1 s). This provides significant evidence that accurate prior information accelerates biological motion perception.

3.2.2.2 Temporal Generalization Analysis Predicting the Location of Biological Motion in Congruent and Incongruent Trials, and Tilt in Neutral Trials

In this analysis, a classifier model was trained on the EEG data from neutral trials at each time point and tested on the EEG data of congruent and incongruent trials. The target of the classifier in this analysis was the location of the biological motion, i.e., which side of the screen it is on (right vs. left). The obtained ROC-AUC values are visualized as a heatmap (Figure 4.14, the left shows the temporal generalization matrix obtained from congruent trials, and the right shows the matrix obtained from incongruent trials).

Next, the temporal clustering test was used to determine the intervals at which the obtained temporal generalization matrices significantly differed from the chance level. Figure 4.15 shows the statistically significant ($p<0.05$) time intervals in Figure 4.14. The gray areas indicate time intervals that are not statistically significant.

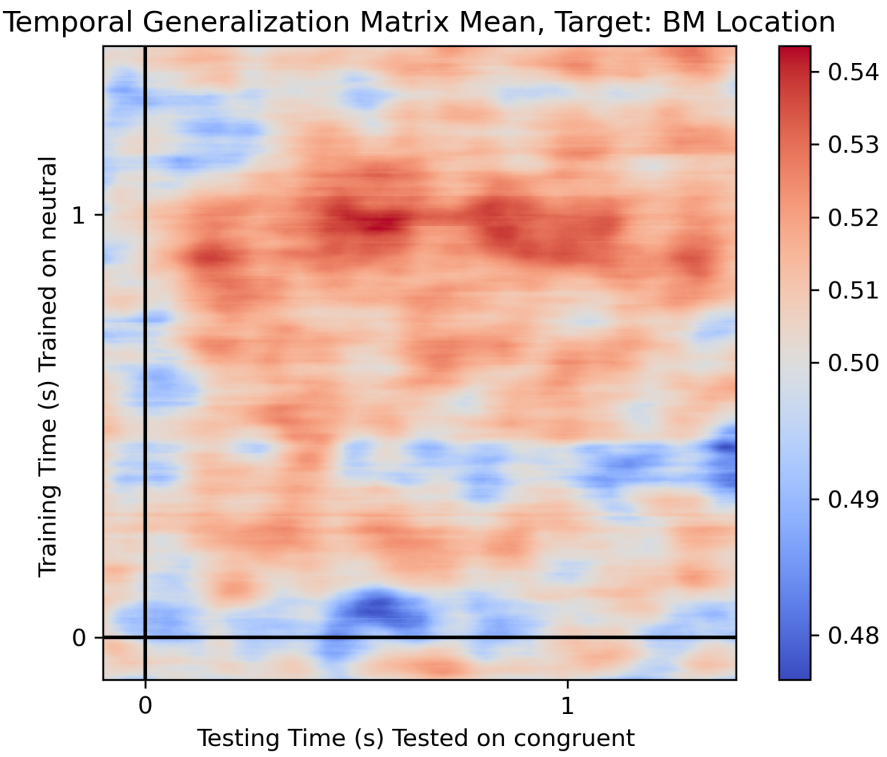

Figure 3.16: The temporal generalization analysis, predicting the type of biological motion in Congruent trials. (The color bar indicates ROC-AUC scores).

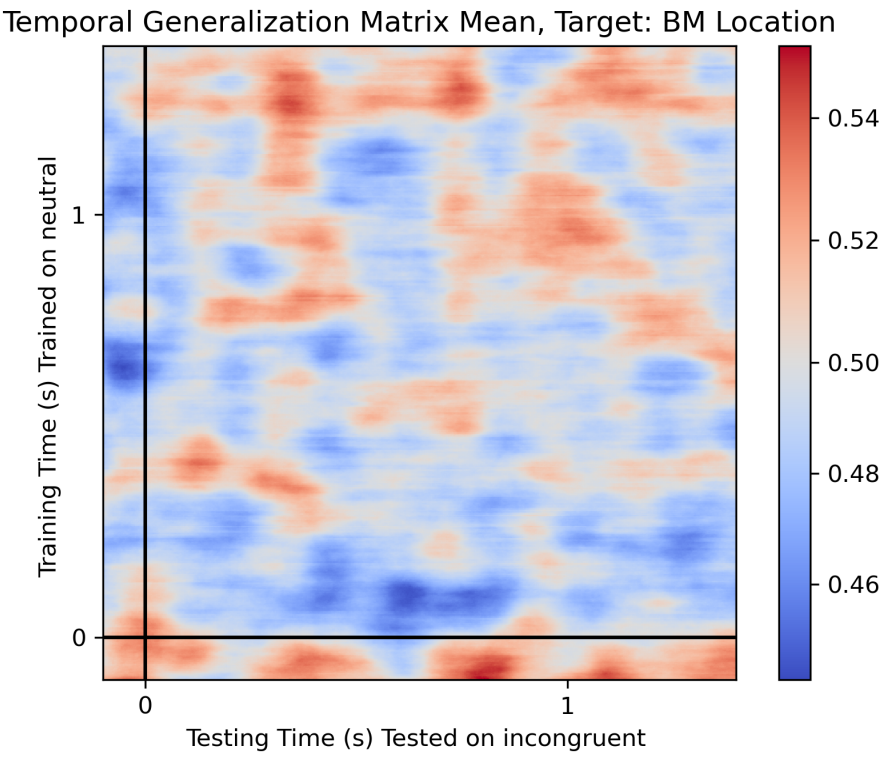

Figure 3.17: The temporal generalization analysis predicting the type of biological motion in Incongruent trials. (The color bar indicates ROC-AUC scores).

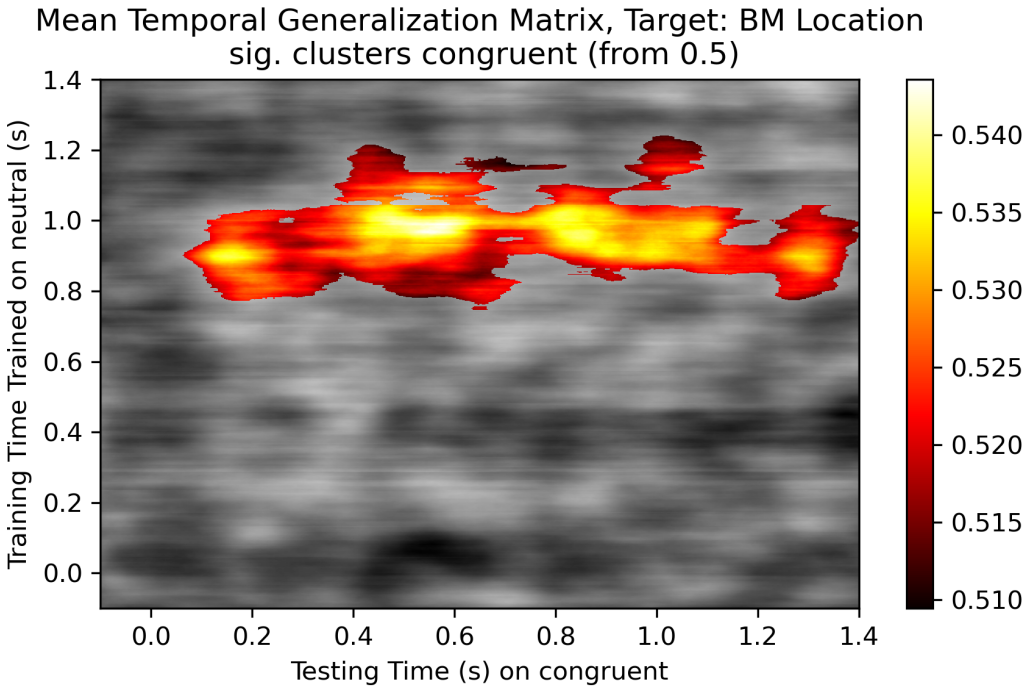

Figure 3.18: Statistical significance of the temporal generalization analysis predicting the type of biological motion in Congruent and Incongruent trials (The color bar represents the roc-auc scores, shows the statistically significant ($p<0.05$) clusters. The gray areas indicate time intervals that are not statistically significant).

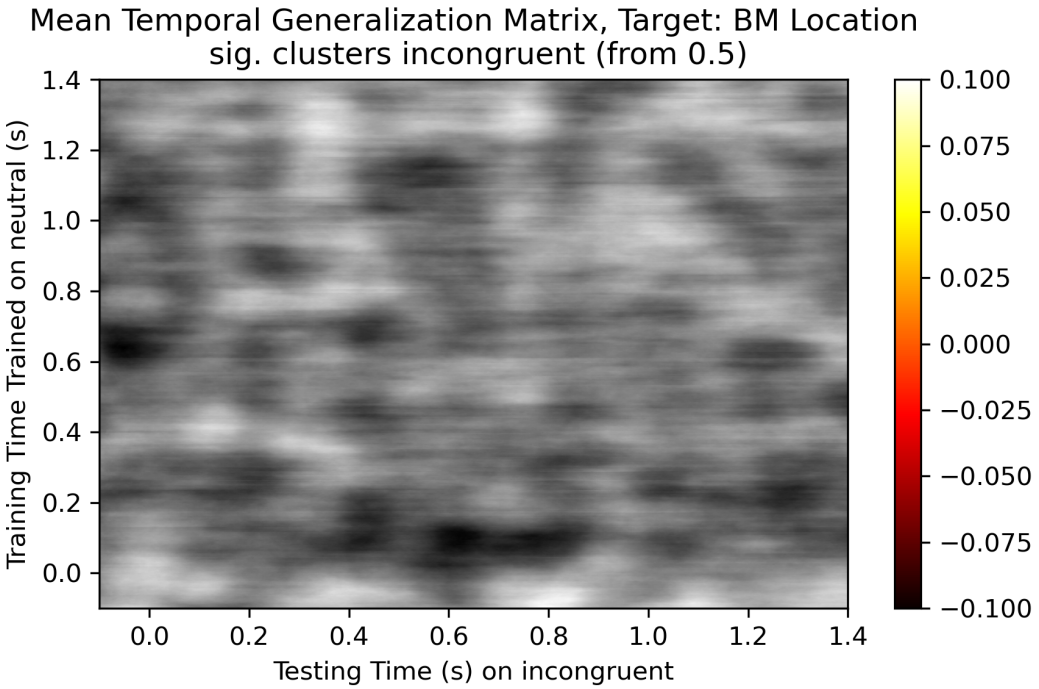

Figure 3.19: Statistical significance of the temporal generalization analysis predicting the type of biological motion in Incongruent trials (The color bar represents the roc-auc scores, shows the statistically significant ($p<0.05$) clusters. The gray areas indicate time intervals that are not statistically significant).

The results of this temporal generalization analysis show that the location of biological motion can only be classified at a statistically higher level than chance in congruent trials. Furthermore, it can be observed from the results that this effect begins at a relatively early time interval (left matrix in Figure 4.15, around 0.1-0.2 seconds). Considering the absence of statistical significance in incongruent trials, this result appears consistent with the previous temporal generalization analysis. According to these results, accurate prior information also enables the location information of the biological motion to form earlier in the brain. Moreover, when comparing the temporal generalization matrices on the type of biological motion (Figure 4.13) and the location of biological motion (Figure 4.15), it can be observed that the location information forms first in the brain, followed by the action type information.

Chapter 4

Discussion

Biological motion perception enables animals to extract various types of information from actions of other animals, which they use to predict others' intentions. Specifically, humans excel at extracting relevant information from biological motion. We can infer the action, emotional state, and gender of others from even a set of dots known as point-light displays, however, the majority of studies with point-light displays investigate bottom-up processing of biological motion and it remains unclear how prior information affects biological motion perception.

4.1 Behavioral Experiments

In the behavioral stage of our project, we examined the impact of prior information on biological motion perception and the factors that may modulate this effect. We specifically explored whether prior information about biological motion features accelerates its processing and individuation if the validity of this information influences perception, and if different types of prior information about different features of biological motion produce distinct effects.

We hypothesized that congruent prior information about biological motion would enhance individuation performance, resulting in faster reaction times in

congruent trials. We also anticipated that increased validity of prior information would amplify its impact on biological motion perception. Lastly, we expected that different information types would produce varying effects on biological motion perception.

We employed a cued individuation paradigm to test these hypotheses, which involved presenting a cue containing information about the forthcoming biological motion stimulus. Participants were presented with point-light display stimuli, a biological motion, and a scrambled motion on the left and right sides of the screen, and they were tasked to locate the biological motion while we measured their reaction time and accuracy. Across three experiments, we manipulated the type of prior information (action category, emotion category, gender category) using different cues. In each experiment, we adjusted the congruency of prior information by modifying the stimulus-cue match. We altered the validity of the prior information by changing the ratio of congruent trials.

Our results show that participants located biological motion faster in congruent trials than incongruent ones when cue validity was high (in 75% condition). Furthermore, we found that this effect was only significant when the prior information was about the action category. No significant differences between congruent and incongruent trials were observed in the other experiments or validity conditions. In this chapter, I will discuss the main findings of our behavioral study.

4.1.1 Prior Information Affects the Individuation of Biological Motion

The literature on predictive processing and expectation suggests that in many tasks (e.g., detection or search), correct and incorrect predictions can significantly impact task performance [62, 29, 45, 44] However, there is little research on how prior information affects socially important and complex stimuli, such as biological motion. Therefore, it is unclear whether there is a predictive effect on biological motion detection.

In our study, we found consistent results with the prediction literature. Our results show that, in the cued individuation task, typically used to measure visual awareness, when the prior information provided by the cue (action category) was correct, biological motion was individuated faster than when the prior information was incorrect. These results demonstrate the effect of correct and incorrect prior information on behavior, as shown in previous studies with simpler stimuli, and extend to more complex and socially significant stimuli. Moreover, since the task was an individuation task, our results suggest that predictive information impacts the processes that enable biological motion to enter visual awareness, consistent with the predictive processing literature [45, 63].

4.1.2 The Validity of Prior Information Modulates Its Effects

The predictive processing literature suggests that the effect of prior information depends on how reliable that information is. Reliable prior information means the predictions are accurate and consistent with sensory information. When prior information is reliable, the brain can confidently use prior information to predict future events. However, if the prior information is unreliable, predictions may be inconsistent or incorrect, and the brain cannot rely on them in decision-making. Therefore, the reliability of expectations is an important factor in predictive processing and decision-making as the brain determines how much weight to give to its prior beliefs when making predictions about the world [38, 64]. Consistent with this view, recent research on prior information and expectation has found that we cannot observe the effects of expectations in behavior when they are not reliably accurate [44]. In the current study, the effect of prior information was observed when the cue was more reliable than the chance level (75% validity condition), but no effect of prior information was observed when its validity was 50%. These results support the literature on expectation and prediction and demonstrate that predictive mechanisms can generalize to biological motion perception.

4.1.3 Different Types of Information Affect Individuation Performance Differently

One significant finding from behavioral experiments is that different types of prior knowledge have distinct effects on the perception of biological motion. When prior knowledge was about emotion or gender information in relation to biological motion, participants' reaction times were not significantly affected. However, participants' reaction times were impacted when the prior knowledge was about action categories. There could be several reasons for this discrepancy.

Firstly, information about actions, gender, and emotions might be processed in different regions or neuronal populations in the brain. Specifically, action recognition primarily involves the activation of the superior temporal sulcus, the premotor cortex, and the parietal cortex, which collectively contribute to perceiving and understanding others' actions [46]. Gender processing, on the other hand, has been linked to the fusiform face area and the extrastriate body area, which are specialized for face and body perception, respectively [65]. Emotion processing, particularly in the context of facial expressions, predominantly occurs in the amygdala, insula, and orbitofrontal cortex, which together facilitate the recognition and interpretation of emotional cues [47, 66]. Consequently, the distinct neural substrates involved in processing action, gender, and emotion information may lead to different behavioral outcomes when integrating such information in the context of biological motion perception. These differences in processing may lead to action information influencing the location detection task, while emotion and gender information do not affect the task.

Secondly, action information may be extracted more quickly and easily from biological motion stimuli compared to emotion and gender information. This might be because our visual system is highly attuned to detecting and interpreting actions, as they provide essential information for social interaction and survival [3]. Neuroscientific research has demonstrated that the human brain possesses specialized neural networks dedicated to processing biological motion, enabling rapid identification of action-related information [67].

In contrast, extracting emotion and gender information from biological motion stimuli may require more extensive processing and integration of additional visual cues. For example, recognizing emotions from body movements often involves the combination of posture, facial expression, and gait patterns, while gender identification relies on the integration of body shape, movement kinematics, and facial features [68, 69]. Furthermore, some of this information is nonexistent in PLD stimuli. As a result, the additional processing steps required for emotion and gender recognition and the lack of additional information, such as facial features and expression, may lead to longer reaction times when compared to action recognition in biological motion perception tasks.

Lastly, the visual stimuli used in the experiment may have made it difficult to differentiate between different types of information. For example, emotion and gender information might be less salient than action information, and participants might have struggled to process these types of information quickly. Results of the norming experiments for gender and emotion stimuli also point to this possibility; while participants could differentiate between these stimuli reliably, the mean scores given were close to 0, and especially for the emotion PLDs, results point that participants may perceive the happy PLD as sad. Therefore the information received from these stimuli may be less salient. This situation may have led to emotion and gender information not significantly affecting participants' reaction times.

4.2 EEG Experiment

In the behavioral study, we observed that accurate and valid prior information about the action category affects the perception of biological motion (Action category experiment, 75% validity condition). To investigate the temporal dimension of the effect of prior information and to conduct a neural investigation of the identified effect, an EEG study with a similar design to the action category experiment's 75% condition was conducted.

4.2.1 Prior Information does not have a Significant Effect on ERPs

Statistical analysis of the ERPs yielded no significant differences between neutral, congruent, and incongruent trials in any electrode or time interval cluster (Figures 3.7 - 3.11. This also meant that we could not find any significant effect of prior information on ERP components that are biological motion sensitive, such as. There could be several reasons for this null effect. Firstly, expectation-based information transfer may be carried by communication at specific frequencies in the brain [70, 71, 39, 72]; therefore, slight differences between conditions may not be observable with the ERP technique. Suppose the effect of prior information is particularly small or spread across different time intervals and electrode regions. In that case, the ERP technique may not be sensitive enough to detect subtle modulations of neural activity related to prior information. Moreover, traditional ERP analysis, which is based on the overall mean value for participants and trials, can obscure the effect of prior information on neural activity by canceling individual or trial-specific effects that are not temporally or spatially consistent [73]. On the other hand, the absence of a prior information effect in ERP analyses is consistent with other EEG studies in the literature [34, 74]. The cognitive processes that integrate prior information with incoming sensory information are complex and multifaceted, which could contribute to the lack of effect found with ERPs. Due to these reasons, alternative techniques and analysis methods, such as time-frequency analysis and multivariate pattern analyses, can provide a more comprehensive understanding of the role of prior information in modulating neural signals of biological motion by improving the analysis of highly varying inter and intra-individual variability.

4.2.2 Prior Information Affects the Neural Processing of the Location and Category of Biological Motion

In the absence of the effect of prior information in the ERP analysis, which contradicted the behavioral results, a temporal generalization analysis was performed on the time-frequency representation of the EEG data across conditions. In this analysis, classifiers were trained at every time point in neutral trials and tested at every time point in congruent and incongruent trials. In two separate classification analyses, we attempted to predict the location of biological motion and the category of biological motion. The results show that the representation of the biological motion category in the brain occurs earlier in congruent trials than in incongruent trials (See figure 3.14 and 3.15, and that accurate prior information accelerates the perception of biological motion by enabling the action category to form at an earlier time interval in the brain.

The results of the second temporal generalization analysis show that the location of biological motion can be classified at a level statistically higher than chance in only congruent trials (See figure 3.19 and 3.18). This can be interpreted as accurate prior information enabling the formation of the location information of biological motion in the brain earlier. On the other hand, it can be observed that this effect begins at a relatively early time interval, even earlier than the time interval obtained in the analysis of the biological motion category. These results support the views of the early effect of prediction on perception, such as [33, 39, 29, 29]

Moreover, considering these two temporal generalization analyses together, it can be said that in the perception of biological motion, the determination of where the biological motion is located is made first, followed by the determination of what the motion is and processes that create both of these representations occur earlier when prior information is congruent rather than incongruent.

4.3 Limitations

The limitations of the current study can be attributed to several factors. Firstly, the lack of significant effects in the gender and emotion experiments in the behavioral study may stem from differences in visibility of the informational cues signaling gender or emotion rather than being intrinsic to the processing or perception of biological motion. Furthermore, it remains unclear how the cue interacts with various processes in the decision-making stage. Although practical, point-light displays (PLDs) may be too simplistic and unnaturalistic to generalize the findings to real-world situations. Additionally, these experiments give no information related to the spatial dimension of these effects or how prior information modulates different brain networks related to decision-making or biological motion perception. Finally, EEG analysis in the study does not provide a potential source for the changes observed with predictive information, such as a specific frequency band; further analysis and experimentation are necessary on this issue.

4.4 Future Directions

To advance our understanding of the effects of prior information on biological motion perception, future research could explore several directions that can also address some limitations of the current study. One such direction involves utilizing more naturalistic stimuli, such as videos featuring real actors, which would provide ecologically valid visual information and enhance the generalizability of the findings. Furthermore, another approach could use computational modeling to understand how prior information alters perceptual and spatial decision-making processes about biological motion. Additionally, future studies could employ neuroimaging techniques functional magnetic resonance imaging (fMRI) or Magnetoencephalography MEG) to gain deeper insights into the spatial neural mechanisms underlying these effects. These methods would enable researchers to investigate both the temporal and spatial aspects of the neural processes involved

in integrating prior information with the perception of biological motion. Finally, the models of biological motion perception can be updated with the temporal information regarding prior information's effect on biological motion. They can be tested on more ambiguous and naturalistic scenarios. By incorporating these approaches, future research can significantly advance our understanding of the cognitive and neural mechanisms underlying the processing of prior information in biological motion perception.

4.5 Conclusion

In this study, we investigated the effects of prior information on biological motion perception and individuation. Our research comprised two components: a behavioral study to explore the impact of prior information on biological motion individuation performance and the factors that influence this effect and an EEG experiment to examine the temporal dynamics of prior information's influence on neural representation and neural processing of biological motion.

Our findings reveal that prior information does indeed impact the individuation of biological motion, but only when the cue pertains to the type of action in the BM stimuli and the cue's validity is high (75%). Furthermore, our results indicate an early influence of predictive information on the visual processing of biological motion. The temporal generalization analysis also suggests that accurate prior information allows for forming location information related to the BM earlier in the brain.

In addition, our analysis of the temporal generalization matrices for the type of biological motion and the location of biological motion demonstrates that location information forms first in the brain, followed by action type information. Importantly, our temporal generalization analysis provides compelling evidence that accurate prior information expedites the perception of biological motion, underscoring the significance of context in shaping our perception of observed actions.

In conclusion, the work done in this project has contributed to the literature in two ways. First, we found that prior knowledge about the action type has temporal and spatial effects on both the behavioral and neural levels of biological motion perception. These findings have highlighted the fact that computational models that aim to explain the mechanisms underlying biological motion perception must consider the effects of prior knowledge. Second, it has shown that prediction-based information processing models, which are increasingly common in the cognitive neuroscience literature, are valid for processing low-level stimuli and can be generalized to biologically and socially significant stimuli, such as biological motion.

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