PREDICTIVE PROCESSING IN THE CORTICAL NETWORK OF BIOLOGICAL MOTION PERCEPTION

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By
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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

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The literature on biological motion processing argues that it occurs in occipitotemporal, parietal and frontal regions of the brain. Nevertheless, the literature is currently unable to explain how this processing is affected by expectations. Although models exist to explain how biological motion is perceived, they usually ignore top-down processes. To this end, the current fMRI study presented two point-light displays (embedded in noise) on either side of the screen to the participants (N=29). One of the displays was a biological motion (walking or kicking) whereas the other one was its scrambled version. The participants were asked to report the location of the biological motion. Importantly, before the presentation of motions, the participants were shown a cue about the action type (walking or kicking) which was congruent with the motion 75% of the time. There were also two additional conditions in which the cue was uninformative about the action (neutral condition) or there were no motion stimuli at all. As expected, the action observation network (consisting of pSTS, parietal cortex and IFG) showed a clear and strong activation during the conditions that a motion was present. However, these regions have failed to significantly discriminate between congruent and incongruent conditions. It should be acknowledged that this lack of significant result might be caused by the low number of trials. In order to better investigate the connections within action observation network, a DCM analysis was conducted. The winning DCM model has successfully shown the presence of feedback connections in the biological motion processing. More specifically, the model argues that both feedforward and feedback modulatory connections are present during congruent, incongruent and neutral conditions. In sum, the study highlights the importance of incorporating top-down signals such as expectations in the computational models of biological motion perception.

Keywords: Biological motion, point-light display, visual perception, expectation, predictive coding.

ÖZET

BEYNİN BİYOLOJİK HAREKET ALGISI AĞINDA TAHMİNE DAYALI KODLAMA

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Nörobilim, Yüksek Lisans
Tez Danışmanı: Burcu Ayşen Ürgen
Temmuz 2024

Biyolojik hareket literatürü, biyolojik hareketin işlenişinin beynin oksipitotemporal, parietal ve ön bölgelerinde gerçekleştiğini savunmaktadır. Ancak mevcut literatür, bu işlenişin tahminler tarafından nasıl etkilendiğini açıklayamamaktadır. Biyolojik hareketin nasıl algılandığını açıklayan modeller bulunsa da bu modeller yukarıdan aşağı süreçleri göz ardı etmektedir. Bu nedenle mevcut fMRI deneyi katılımcılara (N=29) ekranın her iki tarafında birer adet nokta ışıklı uyaran (gürültü noktalarıyla beraber) göstermiştir. Bu uyaranlardan biri biyolojik hareket (yürüme ya da tekme atma) iken diğeri de bu hareketin karıştırılmış versiyonudur. Katılımcıların görevi deney süresince biyolojik hareketin ekranın hangi tarafında belirdiğini bulmaktır. Hareketlerin gösteriminden önce katılımcılar hareketin türüne göre bir ipucu görmüştür (yürüme ya da tekme atma). Bu ipucu, %75 oranında hareket ile tutarlıdır. Ayrıca deneyde iki tane daha koşul bulunmaktadır: ipucunun harekete dair bir bilgi içermediği koşul (nötr koşul) ve herhangi bir hareketin bulunmadığı koşul. Beklenildiği üzere, hareket içeren koşullardan hareket izleme ağında (pSTS, parietal korteks ve IFG bölgelerini içermektedir) kuvvetli bir aktivasyon mevcuttur. Ancak bu bölgeler tutarlı ve tutarsız koşulları birbirinden ayırt etmeyi başaramamıştır. Bu sonucun, deneyin az sayıda deneme içermesinden kaynaklandığı düşünülmektedir. Hareket izleme ağındaki bağlantıları daha iyi incelemek adına DCM analizi yapılmıştır. Analiz sonucunda bulunan kazanan model, biyolojik hareketlerin işlenişinde yer alan geri bildirim bağlantılarını göstermektedir. Model, hem ileri yönlü bağlantıların hem de geri bildirim bağlantılarının tutarlı, tutarsız ve nötr koşullarda var olduğunu göstermiştir. Özet olarak, çalışma biyoloji hareket algısındaki modellerde tahmin gibi yukardan aşağı süreçlerin önemini başarıyla göstermiştir.

Anahtar sözcükler: Biyolojik hareket, nokta ışıklı gösterim, görsel algı, beklenti, tahmine dayalı kodlama.

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Chapter 1

Introduction

1.1 Biological Motion Perception is Essential for Daily Social Life

Biological motion perception is an essential cognitive skill for animal survival. This skill refers to the ability of identifying motion patterns of other biological beings, helping to infer their actions, intentions, and emotions [1]. Evolutionarily, a mastery of biological motion perception is indispensable. For instance, a prey needs to recognize and act appropriately when attacked by a predator, while a predator needs to accurately interpret the actions and intentions of their prey to successfully hunt it. For humans, the ability to perceive biological motion is even more crucial compared to other animals. As inherently social beings, humans rely on biological motion perception since it serves as the foundation of successful social interactions in daily life. For instance, consider a scenario in which one sees a woman rubbing her belly. This action can be interpreted in multiple ways such as she is hungry, she is experiencing a stomachache, or she is pregnant. Effective communication with this woman will not be possible without recognizing the action, identifying necessary social cues, and then combining both to understand the meaning of the action. Although the action itself (rubbing belly) is not categorized as a social action (e.g., talking or waving hand), perception and

processing of the action is necessary for a successful social interaction with that woman [2]. Thus, it is evident that biological motion perception is as significant for daily social functioning as it is for survival.

The importance of biological motion perception for humans has made it a major focus of research in cognitive psychology and neuroscience. Notably, biological motion perception has been shown to be a different cognitive skill than general motion perception [3]. Biological motion perception requires a special neural network known as the action observation network consisting of the posterior superior temporal sulcus (pSTS), posterior parietal cortex (PPC), and inferior frontal gyrus (IFG) [4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14]. Albeit not a part of the AON, it is also worth noting that some studies found selectivity for biological motion in the fusiform gyrus as well [15]. Further showing its evolutionary importance, the network appears to be innately active. Newborn babies have a preference for attending to biological motion, and they become able to detect characteristics of biological motion (such as direction) as early as three months old [16, 17, 18]. Additionally, even newborn chicks without any prior visual experience were seen to exhibit a clear preference for biological motion over non-biological motion [19]. However, the ability to perceive biological motion is argued to decline with age as older adults are generally slower at biological motion perception compared to younger adults [19, 20]. Additionally, the activation of the action observation network also depends on the task. The full network is activated when the participants actively attend to the biological motion. However, if the biological motion is given to the participants as a distractor that they need to ignore, then the activation is only observed in lower-level visual processing areas such as the extrastriate body area, human middle temporal complex, fusiform face area, and STS [4, 21, 22].

1.2 PLDs: A Special Type of Stimulus for Studying Biological Motion Perception

While studying biological motion perception, special stimuli called point-light displays (PLDs) are often used. These displays are created by attaching light-emitting markers to the joints of a moving person dressed in a dark suit. As a result, a display of moving lights is obtained, which is known to be enough for activating the action observation network and for successful perception of the motion [1, 9, 23]. Using point-light displays in biological motion perception studies enables a highly valid and controlled investigation of the motion by isolating the motion itself from other visual information and cues such as face, gender, emotion, age, and race [1, 9, 23]. Nevertheless, when necessary, it is possible to integrate desired social information into the display. Research has shown that, when manipulated appropriately, participants are able to understand social information such as gender, emotion, and age from the point-light displays alone [24, 25, 26]. Consequently, by using point-light displays, the experimenters can manipulate the motion information (or any social information) without worrying about potential confounding factors. Point-light displays for almost any desired action can be obtained from publicly open online databases.

According to the demands of the research question, researchers often add certain manipulations to the point-light displays. In order to prevent ceiling effects, a common manipulation is to add noise in the form of randomly moving dots. Jastorff and Orban [4] have shown that the participants are still able to correctly recognize the biological motion even if it is accompanied by a high level of noise. As mentioned before, biological motion perception is different from general motion perception. Therefore, another commonly utilized manipulation in biological motion studies is the use of a scrambled version of the biological motion as a control stimulus. Scrambled motions are obtained by randomly changing the starting points of dots in a point-light display without altering their movement trajectories. This way, a new stimulus is obtained which is mostly identical to the biological motion in terms of low-level information (randomly moving dots) but different in terms of high-level information (whether or not it forms a biological

motion). Scrambled motions have been shown to be a valid control stimulus as they do not activate brain regions (pSTS) that are active during biological motion perception [27].

1.3 Is Biological Motion Perception a Bottom-Up or Top-Down Process?

Although the addition of scrambled motions and noise dots allowed a more controlled investigation of biological motion perception, they were still not enough to prevent high accuracy scores of the participants. The participants were extremely fast and accurate in the perception of biological motion, even in tasks with high noise levels [9, 28]. The ease in its processing has led researchers to believe that biological motion perception is an automatic process modulated solely by bottom-up information. As such, emphasis on bottom-up processes in biological motion perception studies has become a recurring pattern. Most notably, the importance of feet information for biological motion perception was investigated in these studies. During these studies, participants were presented with point-light displays. However, only a specific body part of the display was visible while the rest of the body was occluded. The participants were able to successfully recognize the direction of the motion only when the feet were visible to them [29, 30]. As a result, the researchers argued that feet information alone was enough for biological motion perception. According to them, this was because the motion of the feet was triggering necessary innate cognitive mechanisms for biological motion perception, recognition, and interpretation [29, 30]. These findings argue that biological motion perception is driven by sensory input rather than feedback information, highlighting the role of bottom-up processes.

The importance of bottom-up processes in biological motion perception also found its place in the presented models. The first model presented by Johansson [1] suggests that biological motion perception is a hierarchical mechanism that utilizes only feedforward information. According to the model, minimal and simple motion cues are integrated into the perception of biological motion [1]. Similarly, the model presented by Giese and Poggio [31] argues that low-level

motion information is integrated into more complex information to be compared against specific motion templates. These templates, stored in neurons specifically tuned for motion perception, allow the correct perception and interpretation of the biological motion. The authors also note that, albeit not necessary for perception, feedback connections and top-down processes may be present depending on the task [31]. These models are able to successfully explain biological motion perception in the majority of the tasks. However, they fail to acknowledge that observing a stimulus in daily life is remarkably different from observing it in an experimental setting. In daily life, one's perception is constantly affected by top-down processes, most notably attention and expectation. Thus, researchers started to challenge the view that biological motion perception is solely a bottom-up process. To that end, the role of attention in biological motion perception was studied through multiple studies. These studies used Lavie's [32] attentional load theory as a basis. According to him, attention is a limited resource and multiple stimuli continuously compete for one's attention. Thus, it is essential to selectively focus on a particular stimulus to effectively process it [32]. Using this theory as a basis, the effect of attention on biological motion perception was investigated through multiple studies. Findings show that, aligning with Lavie's theory, attending to a biological motion stimulus significantly facilitates its processing. On the other hand, when participants are unable to attend to the biological motion because their attention is directed elsewhere (particularly to a task with high attentional load), their perception of biological motion will be noticeably impaired or even prevented [33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44].

1.4 Expectations Create Perception

Although the effect of attention on biological motion perception has been investigated, the effect of prediction remains unexplored. Nevertheless, prediction literature proposes significant evidence to demonstrate how our expectations about a stimulus shape the perception of that stimulus. The review article written by de Lange and colleagues [45] provides multiple examples of how prior information is combined with sensory input to form, alter, or impair the perception of stimuli.

A famous example, the McGurk effect, can be described as the alteration of auditory perception when the auditory input does not meet the expectations created by the visual input [46, 47]. The effect of predictive coding on perception is also observed in experimental settings. When the participants are given correct prior knowledge about a stimulus, behavioral and fMRI studies show that they will process this stimulus more accurately, more effectively, and more efficiently [48, 49, 50]. fMRI studies have also revealed that the prefrontal cortex and medial temporal lobe play a role in the generation of predictions based on prior knowledge [51, 52]. However, when the generated predictions are not met, a feedback signal is created in the brain that stores the differences between expected input and actual input. This signal, called the prediction error, is created with the help of the ventral tegmental area (VTA), anterior cingulate cortex (ACC), striatum, and prefrontal cortex [51, 53, 54, 55, 56].

These experiments show clear evidence for the idea that expectations shape our perception. However, there exists a big gap in the literature: Expectation studies have mostly preferred the utilization of low-level and simple stimuli. In terms of visual expectation, these stimuli showed themselves in the form of Gabor filters or moving dots. The utilization of such elementary stimuli was advantageous in order to investigate the neural basis of expectation while removing potential confounding factors. Nevertheless, they lacked considerable external validity. In nature, animals are highly unlikely to find themselves in a situation in which they are required to make an expectation based on Gabor filters. Ultimately, it is mostly unknown if there is a difference between the effect of expectation on low-level stimuli and complex stimuli. More specifically, the effect of expectation on socially meaningful stimuli is yet to be explored.

One of the previous studies that aimed to fill this gap utilized face and house stimuli preceded by a cue with varying levels of congruency [57]. The findings have shown that, similar to the studies that utilized low-level stimuli, visual processing of the stimulus was slower during the conditions in which expectations were not met [57]. Nevertheless, the effect of predictive coding on biological motion perception has not yet been investigated until Elmas and his colleagues [58] conducted a behavioral and EEG study. In their study, the researchers used cues

followed by biological and scrambled motions. In the span of multiple behavioral experiments, different types of cues (type of action, gender, and emotion) were presented at different cue congruency levels (0%, 50%, 75%, and 100%). The EEG study was conducted by using cues about the action type with 75% congruency as this was the only condition during which a behavioral effect of congruency had been observed. Specifically, the participants were faster at recognizing the biological motion in congruent conditions. Although the EEG variation of this study revealed important information about the early influence of predictive processing on biological motion perception, spatial neural information of this influence is yet to be analyzed [58].

1.5 Aim of the Current Study

Ultimately, two gaps in different literatures have been identified. The biological motion literature is believed to be in need of studies that show the influence of top-down processes in its perception. Although the top-down influence of attention on biological motion perception was shown by previous studies, the top-down influence of prior information on biological motion perception still remains unexplored. As prior information has been shown to affect our perception, the current study believes that its effect on biological motion perception should be investigated in detail [48, 49, 50]. Similarly, prior information literature lacks studies that utilize socially meaningful stimuli. Prediction studies with socially meaningful stimuli are essential for generalizability of the results as well as for interpretation and implication of the findings in daily-life scenarios. Thus, the current study believed that combining biological motion perception and prior information literature is essential to have a deeper understanding of both of the processes. Nevertheless, no study except Elmas and his colleagues [58] aimed to investigate the question of how prior information affect biological motion perception. The current study intended to explore this question. In a methodical framework, the study was an fMRI variation of Elmas and his colleagues' [58] EEG study while also building on it by multiple fMRI analysis techniques. Although Elmas and his colleagues has contributed to the literatures in multiple ways by showing temporal aspects of prior information's influence on biological

motion perception, their study lacked in showing spatial information of that influence. In order to investigate it, the current fMRI study utilized a prediction paradigm in which biological motion is presented to the participants preceded by a cue about the motion's action type. Then, the data was analyzed with general linear model (GLM), multivariate pattern analysis (MVPA) and dynamic causal modeling (DCM) methods. GLM analysis was performed in order to compare the brain data between experimental conditions. Similarly, MVPA was performed to support GLM results by exploring the brain regions that were able to differentiate between experimental conditions. Lastly, DCM analysis was performed to create a model that explains the strength and direction of connections in the action observation network during the observation of a biological motion. In doing so, the study aimed to contribute to the literature by creating a new model that explains the role of feedback connections as well as being the first model that includes effects of prior information. In all of the analyses, a difference was expected to be observed between experimental conditions that creates a correct prediction and a violated prediction.

Chapter 2

Methods

2.1 Participants

fMRI data of 29 participants was collected (Range = 18-30, Mean = 22.6, Standard deviation = 3.0, 17 female, 12 male). Before the experiment, the participants were fully informed about the procedure and gave their informed consent. After the experiment, the participants were compensated with either money (50 TL) or course credit, depending on their choice.

2.2 Stimuli

Two types of stimuli were used in the experiments: Cue stimuli and point-light displays. The cue stimuli had three variations: The image of a walking man, the image of a kicking man, and the image of a question mark. Similarly, the point-light displays had four variations: The biological motion of a kicking man, the scrambled display of a kicking man, the biological motion of a walking man, and the scrambled display of a walking man. Each display consisted of 13 dots and the scrambled displays were created by randomizing the starting point of each dot from the original display (Figure 2.1). The study decided to focus on walking and kicking actions for two main reasons, despite other possible actions being considered. First, based on previous literature, feet information is

essential for biological motion perception [28, 29]. Therefore, the selected actions were required to show clear but distinct feet movements. Second, researches have shown that processing of communicative actions differs from processing of non-communicative actions [59, 60]. Thus, since the current study is only interested in the processing of motion information independent of communicative intent, non-communicative actions were required to be selected. Ultimately, walking and kicking actions were found to be ideal for the current study as these actions had clear but distinct feet movement and both of them were non-communicative actions. The cue stimuli were 3.5 x 3.5 degrees in size and were presented at the center of the screen. On the other hand, the point light displays were 5.2 x 8.3 degrees in size and were presented at 6 degrees to the left or right of the center.

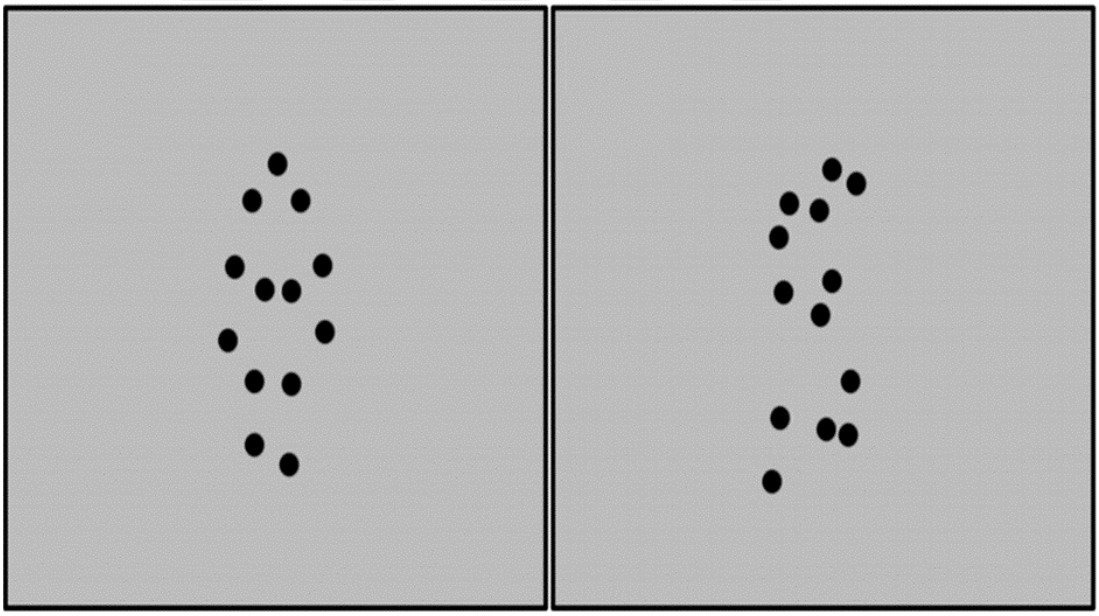

Figure 2.1: Point-light Displays.
Note: Figure at the left represents the walker and figure at the right represents its scrambled version.

2.3 Experimental Design and Procedure

The experiment was coded in MATLAB with the help of PsychToolBox and Biomotion Toolbox [61, 62, 63]. Each run of the experiment consisted of four

conditions: Congruent, incongruent, no cue (neutral), and blank. A congruent trial would follow these steps (Figure 2.2): Firstly, the walking man or kicking man cue was presented to the participants for 2 seconds. Then, there was an interstimulus interval ranging from 0.5 to 1.5 seconds. Following this, a point light display was presented on the left and right sides of the screen for 1.7 seconds. One of the displays was a biological motion and the other one was its scrambled version. However, both of the displays were consistent with the cue. After the stimulus period, the participants were asked to indicate on which side (left or right) the biological motion (not the scrambled motion) was presented. The responses of the participants were collected using the left and right buttons of an MRI-compatible button box. The response period lasted for 2 seconds, followed by a feedback period of 1 second during which the participants were informed that their response was either correct, incorrect, or miss (no response). Before the next trial, there existed another interstimulus interval ranging from 3 to 4 seconds. In total, each trial lasted between 10.2 to 12.2 seconds. Moreover, at the center of the screen, a black plus sign was used as a fixation throughout the experiment. After the motion stimuli, this fixation turned to white for 2 seconds in order to indicate to the participants that they were in the response period. Before the experiment, the participants were instructed to always fixate on the fixation point and respond only when it turned white.

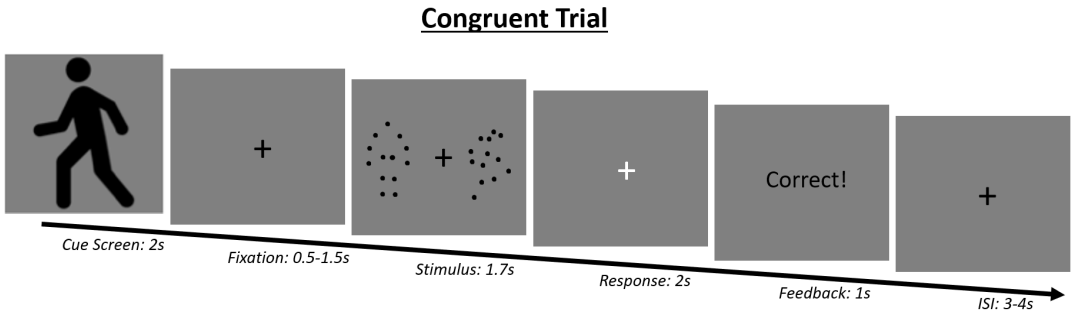

Figure 2.2: An example congruent trial

The other conditions would follow the same steps as the congruent condition but with minor differences. During the incongruent condition, the point light displays that the participants saw were inconsistent with the cue that had been

presented (Figure 2.3). On the other hand, during the no cue condition, the cue that was presented was an image of a question mark so that it would include no information about the following displays (Figure 2.4). During the blank trials, a cue was presented to the participants but no display followed it. Instead, the fixation point was shown to the participants ranging from 8.2 to 10.2 seconds (Figure 2.5). Naturally, the participants were not expected to give a response during blank conditions. An example cue-display pair for a congruent trial would consist of a walking man image followed by a walking man motion and its scrambled version. For an incongruent trial, it would consist of a walking man image followed by a kicking man motion and its scrambled version. An example pair for no cue trials would consist of a "?" image followed by a kicking man motion and its scrambled version. Lastly, for blank trials, it would consist of a walking man image followed by a long period of fixation.

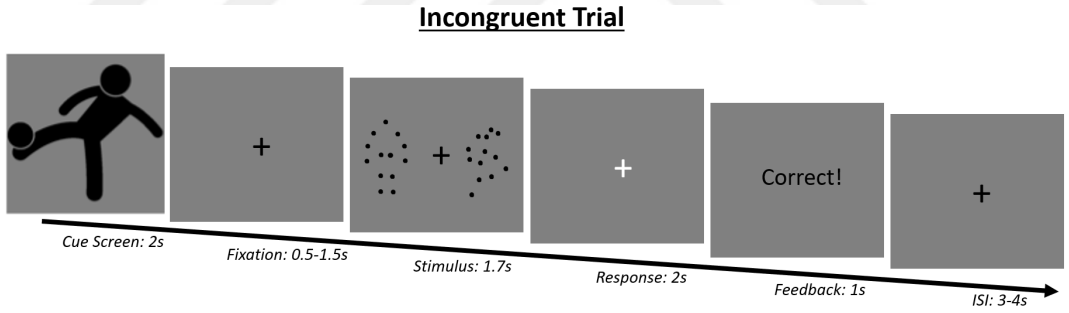

Figure 2.3: An example incongruent trial

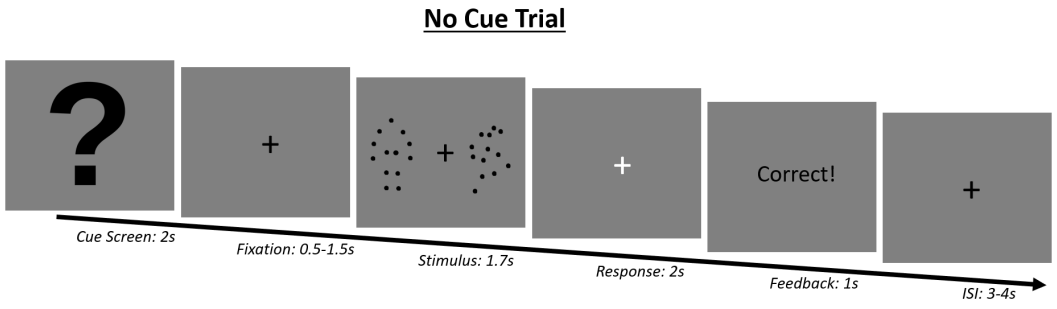

Figure 2.4: An example no cue trial

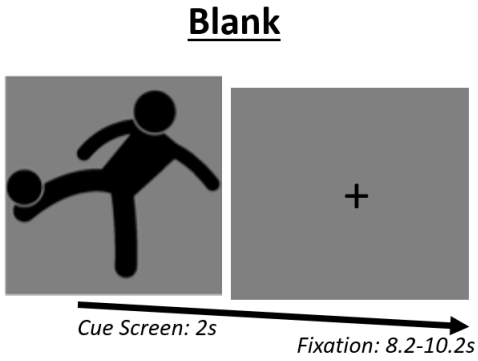

Figure 2.5: An example blank trial

The experiment was designed to have a 75% congruence rate. In order to achieve this rate, each run consisted of 12 congruent trials and 4 incongruent trials. In terms of cue-stimulus pairings, the kick-kick pair and walk-walk pair were each presented in 6 of the trials. Similarly, the kick-walk pair and walk-kick pair were each presented in 2 of the trials. The control conditions, which are no cue and blank conditions, were presented in the same amount as the incongruent trials. The ?-kick pair, ?-walk pair, walk-blank pair, and kick-blank pair were each presented in 2 of the trials. Therefore, each run would last for 24 trials. Moreover, a rest period of 10 seconds was added at the beginning and end of each run during which the participants were instructed to fixate on the fixation point. Ultimately, each run lasted for 5 minutes and the experiment spanned 10 runs. Between runs, the participants were free to rest their eyes as long as they wanted.

In order to prevent ceiling performances, a set of randomly moving dots was added to the experiment as noise. To determine the optimal noise level and ensure that participants understood the procedure, they were asked to complete a short behavioral practice period before the experiment. The practice period started with detailed instructions for the experiment. Then, the biological motions and scrambled motions were introduced to the participant. This was followed by the first practice experiment, which was an 80-trial version of the original experiment. This version had shorter interstimulus intervals (ranging from 0.8 to 1.2 seconds)

and did not contain the blank condition. Moreover, the Quick Estimation by Sequential Testing (QUEST) method was used to adaptively calculate the ideal amount of noise during this practice. At the end of this experiment, QUEST determined the optimal noise level for that participant, which would be utilized throughout the original experiment. Once the participants were done with this practice, they moved on to the second practice experiment. This version consisted of 14 trials and was an exact replica of the original experiment in terms of trial durations, noise level, and blank conditions. Throughout the practices and the fMRI experiment, the participants were instructed that their priority should be to respond as accurately and quickly as possible, with an emphasis on correct answers.

2.4 fMRI Data Collection

A 3T Siemens TimTrio MRI scanner and 32-channel head coil in National Magnetic Resonance Research Center (UMRAM, affiliated with Bilkent University) were used for the scanning periods. In order to prevent the participants from moving their body parts, foam sponges were placed under their heads, on the sides of their necks, and under their legs. A mirror was placed on top of the head coil to allow participants to see the MRI-compatible LCD screen (TELEMED, 60Hz refresh rate, 800x600 pixels, 32 inches). The participants would see the stimulus on this screen from a distance of 168 cm. Before the experiment began, high-resolution T1-weighted anatomical scans of the whole brain were taken. Their parameters were as follows: TE = 2.92ms, TR = 2.6s, flip angle = 12°, acceleration factor = 2 (176 sagittal slices with a resolution of 1mm x 1mm x 1mm). Functional scans were acquired using EPI sequences during the experiment. Their parameters were as follows: TE = 30ms, TR = 2s, flip angle = 90°, 240 field of view, 96x96 matrix, 49 horizontal slices with a thickness of 2.5mm. Each scan started with 3 dummy scans to ensure the scanner reached a stable level.

2.5 fMRI Data Analysis

2.5.1 Preprocessing

Preprocessing was conducted using fMRIPrep 20.1.1, based on Nipype 1.5.0 [64, 65]. Preprocessing steps were motion correction, slice-timing correction, registration, and normalization. Motion correction was performed using mcflirt by estimating head movements at 3 dimensions and 2 directions [66]. Slice-time correction was performed using 3dTshift from AFNI 20160207 [67]. Registration was performed using bbregister, with 6 degrees of freedom [68]. ICBM 152 Nonlinear Asymmetrical template version 2009c was selected for spatial normalization [69].

2.5.2 General Linear Model (GLM)

The first analysis to be conducted on the model was the general linear model (GLM). The SPM12 toolbox of MATLAB was utilized for this analysis. 20 regressors were determined for each participant. In order, these regressors were: Cue, After cue interval, congruent condition with kick-kick pairing, incongruent condition with kick-walk pairing, incongruent condition with walk-kick pairing, the congruent condition with walk-walk pairing, no cue condition where the motion is kicking, no cue condition where the motion is walking, blank condition where the cue is kicking, blank condition where the cue is walking, response period, feedback period, inter-trial interval, and rest period. The last 6 regressors were head movements of the participant in 3 dimensions and 2 directions.

2.5.3 Multivariate Pattern Analysis (MVPA)

To obtain stronger results, the data underwent a machine learning analysis method called multivariate pattern analysis. The Decoding Toolbox of MATLAB was utilized for this analysis [70]. As a result of the 75% congruence nature of the experiment, the experiment included more congruent trials than incongruent, no cue, and blank trials. In order to prevent this situation from causing problems during the training phase of MVPA, only 1/3 of randomly selected congruent trials were analyzed for each participant. Half of these trials were chosen from congruent trials with kick-kick pairing whereas the other half were chosen from

congruent trials with walk-walk pairing. MVPA was conducted by the searchlight method, using a sphere of 4mm radius. Cross-validation was done by leave-one-run-out method and Support Vector Machine was used as classifier.

2.5.4 Dynamic Causal Modeling (DCM) Analysis

Dynamic Causal Modeling is an fMRI analysis method to explore the strength and direction of connections between regions of interests [71, 72]. The technique includes two stages: Model specification and model selection. Model specification stage consists of the creation of models with connections based on previous literature and current hypotheses. Then, the endogenous and modulatory connections between regions of interests are estimated for each model. This stage is followed by the model selection stage, which includes Bayesion Model Selection procedure to calculate each model's probability to explain the current data. Then, the most probable model is declared as the winning model. For the current study, this technique was decided to be used to deeply explore the action observation network. The nodes of action observation network (inferior frontal gyrus, posterior superior temporal sulcus and posterior parietal cortex) were defined as regions of interests, connections among these regions were modelled in model specification stage and the model that is most likely to explain the data was selected in model selection stage.

2.5.4.1 Definition of Regions of Interest

Importantly, only the first 8 runs of each participant were used for ROI definition. 8 participants' data failed to have 10 runs as 4 participants asked to end the experiment prematurely after 8 runs and 5 participants (one of which asked to end the experiment early) had 1 or 2 of their runs excluded from fMRI analysis because of head motion. Since DCM analysis required the same number of runs among participants, it was decided that only the first 8 runs of each participant would be included in the DCM analysis. Moreover, for a more consistent ROI definition, DCM and ROI analyses were decided to be conducted on the same runs, which resulted in 8 runs for ROI definition. A new GLM was conducted to define regions of interest (ROI). 11 regressors were used for this GLM. They were, in

order: Congruent condition, incongruent condition, no cue condition, blank condition, and rest. Once again, the last 6 regressors were head movements of the participant in 3 dimensions and 2 directions. For each participant, a contrast was created by subtracting the blank condition from the combination of congruent, incongruent and no cue conditions. This contrast of motion conditions with non-motion condition was decided to be used for definition of ROIs. Since the aim of DCM analysis was to investigate the connections within the action observation network, nodes of AON (pSTS, PPC and IFG) were pre-determined as ROIs. Therefore, the activation of created contrast was investigated in these nodes. Indeed, the second level GLM analysis has shown activation at inferior frontal gyrus (IFG), posterior superior temporal sulcus (pSTS) and posterior parietal cortex (PPC). AAL atlas of SPM12 was utilized to determine the active brain regions [73]. Although the activation was bilateral, activation at right nodes were stronger compared to left nodes. Therefore, the following brain regions were defined as ROIs: Right IFG ($x = 54, y = 12, z = 27$), right pSTS ($x = 48, y = -52, z = 4$), and right PPC ($x = 27, y = -55, z = 54$)($p < 0.01, \text{not corrected}, k = 0$). Then, a sphere of 5mm radius was determined at each ROI for each participant. The local maxima within this sphere served as the center point for a sphere of 4mm radius, specific to each participant. Principal eigenvariate of all voxels that survived $p < 0.01$ threshold within that sphere was used to extract ROI time series for each run. Ultimately, ROIs were selected on the first 8 runs of 21 participants. 7 participants had to be excluded from ROI and/or DCM analysis because of the following reasons: One participant's data contained only 7 runs, two participants' data were invalid because of head motion, two participants' data failed to show activation in the selected ROIs, and three participants' data were invalid because of a technical problem with the MRI scanner.

2.5.4.2 Model Specification

DCM analysis was conducted by the SPM12 toolbox of MATLAB. The analysis consisted of two steps: Model specification and model selection. Model specification required the creation of models in order to explain current data, under the light of previous studies and current hypotheses. This step was followed by model selection, during which the most probable model (called the "winning model")

was selected by the Bayesian Model Selection procedure. In order to explain the current data, 64 models were created. These models aimed to address how different conditions (congruent, incongruent, and no cue) modulate the connections between pSTS, PPC, and IFG. Based on previous literature, all models assumed that information first enters the pSTS and then follows a feedforward flow from pSTS to PPC and from PPC to IFG. On the other hand, the presence of feedback connections was different among models. The general model, which included every possible connection of interest in the study, proposed that all 6 possible feedback connections were present alongside the feedforward connections. These connections were: The feedback connection from PPC to pSTS that was modulated by congruent condition, the feedback connection from PPC to pSTS that was modulated by incongruent condition, the feedback connection from PPC to pSTS that was modulated by no cue, the feedback connection from IFG to PPC that was modulated by congruent condition, the feedback connection from IFG to PPC that was modulated by incongruent condition, and the feedback connection from IFG to PPC that was modulated by no cue condition. Every other model was then obtained by removing at least one feedback connection from this model, resulting in 64 possible models. Then, the models were grouped into 8 families. Connections from PPC to pSTS were different for models among different families whereas connections from IFG to PPC were different for models within the same family (Table 2.1).

Table 2.1: 64 DCM Models

	PPC --> pSTS IFG --> PPC							
Family 1	C I ? C I ?	C I ? C I	C I ? C ?	C I ? I ?	C I ? C	C I ? I	C I ? ?	C I ? X
Family 2	C I C I ?	C I C I	C I C ?	C I I ?	C I C	C I I	C I ?	C I X
Family 3	C ? C I ?	C ? C I	C ? C ?	C ? I ?	C ? C	C ? I	C ? ?	C ? X
Family 4	I ? C I ?	I ? C I	I ? C ?	I ? I ?	I ? C	I ? I	I ? ?	I ? X
Family 5	C C I ?	C C I	C C ?	C I ?	C C	C I	C ?	C X
Family 6	I C I ?	I C I	I C ?	I I ?	I C	I I	I ?	I X
Family 7	? C I ?	? C I	? C ?	? I ?	? C	? I	? ?	? X
Family 8	X C I ?	X C I	X C ?	X I ?	X C	X I	X ?	X X

Note: Each model proposed that feedforward connections were present during every condition from pSTS to PPC and from PPC to IFG. In each cell, elements in the top represent connections from PPC to pSTS whereas elements in the bottom represent connections from IFG to PPC. C = Congruent condition, I = incongruent condition, ? = no cue condition, X = no connection.

Chapter 3

Results

3.1 Behavioral Results

8 runs across 4 subjects were excluded from the behavioral analysis because the participants were unable to successfully complete them.

3.1.1 Practice Session

Throughout the first practice experiment, Quick Estimation by Sequential Testing method was used to adaptively calculate the ideal noise level (i.e. number of noise dots used) for that participant. The range of noise level was found to be from 8 to 160. However, it is important to acknowledge that the second highest noise level was 43. The average noise level was calculated to be 23.76, with a standard deviation of 28 (Table 3.1).

Table 3.1: Number of Noise Dots Used Per Participant

Subject No	Noise Level
1	22
2	22
3	22
4	10
5	40
6	29
7	10
8	31
9	10
10	10
11	22
12	35
13	160
14	14
15	8
16	25
17	20
18	10
19	16
20	8
21	11
22	30
23	43
24	9
25	13
26	8
27	16
28	16
29	19

3.1.2 Accuracy Results

Repeated measures ANOVA was applied to the accuracy results. Missed trials were treated as incorrect responses for the purposes of accuracy analysis. Mauchly's test of sphericity indicated that the assumption of sphericity had been violated ($p < 0.05$). Therefore, Greenhouse-Geisser correction was applied to the data. The corrected results showed a main effect of the condition. There was a significant difference among congruent (Mean = 75.2%, SE = 2.2%), incongruent (M = 71.7%, SE = 2.9%) and no cue (M = 78.8%, SE = 1.9%) conditions in terms of accuracy ($F(1.619,45.322) = 8.410$, $p = 0.002$, $\eta_p^2 = 0.231$). Post hoc tests revealed that participants were significantly more accurate during no cue condition compared to incongruent condition ($t(28) = 4.101$, $p < 0.001$). No difference was

observed between congruent and no cue conditions nor between congruent and incongruent conditions ($p = 0.088$ for both). P-values were adjusted for family comparison during post hoc tests (Figure 3.1).

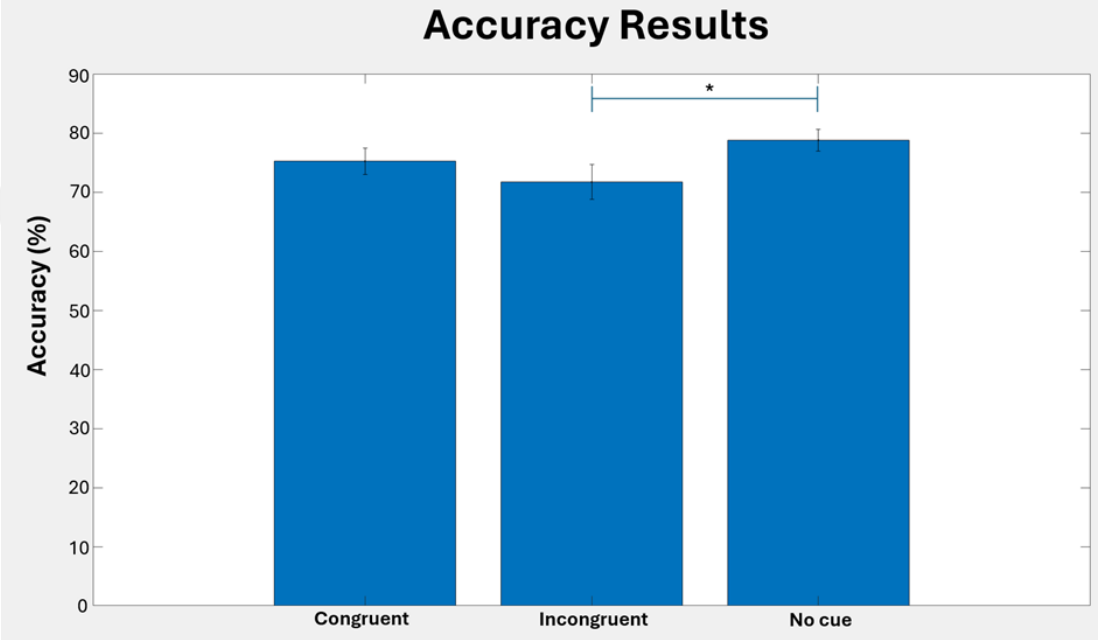

Figure 3.1: Accuracy Results

3.1.3 Reaction Time Results

Repeated measures ANOVA was applied to the reaction time results for correctly answered trials. The results showed the main effect of the condition. There was a significant difference among congruent (M = 0.572, SE = 0.023), incongruent (M=0.615, SE = 0.026) and no cue (M=0.611, SE = 0.029) conditions in terms of reaction time ($F(2,56) = 8.284$, $p < 0.001, \eta_p^2 = 0.228$). Post hoc tests revealed that participants were significantly faster during congruent condition compared to incongruent condition ($t(28) = -3.677$, $p = 0.002$) and compared to no cue condition ($t(28) = -3.350$, $p = 0.003$). No difference was observed between incongruent and no cue conditions ($p = 0.745$). P-values were adjusted for family comparison during post hoc tests (Figure 3.2).

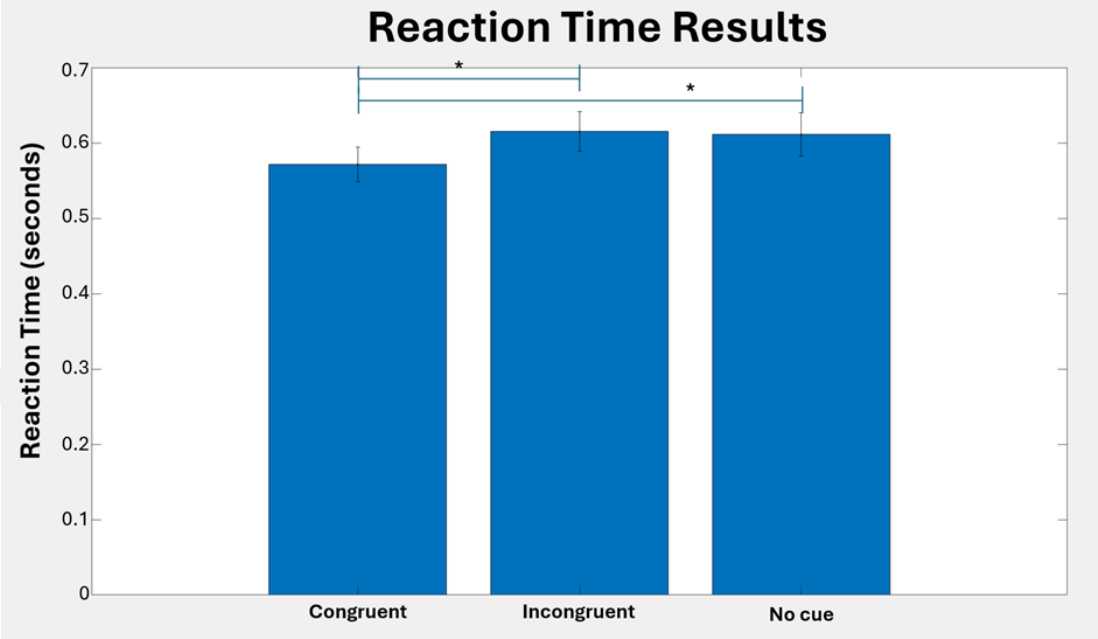

Figure 3.2: Reaction Time Results

3.2 GLM Analysis

5 participants had to be excluded from GLM analysis because of the following reasons: 2 participants' data were invalid because of head motion and 3 participants' data were invalid because of a technical problem with the MRI scanner. Second level GLM analyses were conducted for the following condition pairs: Congruent and incongruent, congruent and no cue, incongruent and no cue, blank and congruent, blank and incongruent. Moreover, congruent and incongruent conditions were combined and this combination was paired with blank and no cue conditions to create two new pairs. Each pair was analyzed twice, once during which the first element was subtracted from the second element and once during which the second element was subtracted from the first element. Ultimately, 14 GLM contrasts were created and analyzed in the second level (Table 3.2). The results showed that there were no significant differences for the pairs that did not contain the subtraction of the blank condition ($p > 0.05, \text{FWE-corrected}, k = 5$ for all). However, a difference was observed when blank condition is subtracted

from congruent condition, incongruent condition and the combination of congruent and incongruent condition ($p < 0.05$, FWE-corrected, $k = 5$ for all) .

Table 3.2: GLM Local Maxima Values

	GLM Results					
	Left			Right		
	Congruent	Incongruent	Congruent+ Incongruent	Congruent	Incongruent	Congruent+ Incongruent
IFG	x=-30 y=26 z=6			x=30 y=30 z=2	x=32 y=30 z=-4	x=32 y=32 z=2
SPL	x=-34 y=-52 z=49	x=-28 y=-48 z=42	x=-34 y=-52 z=49	x=26, y=-52 z=54	x=26 y=-52 z=52	x=26 y=-52 z=54
SOG	x=-28 y=-76 z=24					
Thalamus Proper					x=12 y=-16 z=9	x=12 y=-16 z=9

Note: $p < 0.05$, *FWE-corrected*, $k = 5$ *for all.*

3.3 MVPA

5 participants had to be excluded from MVPA because of the following reasons: 2 participants' data were invalid because of head motion and 3 participants' data were invalid because of a technical problem with the MRI scanner. In line with the GLM analysis, 7 pairs were created for MVPA analysis: Congruent and incongruent, congruent and no cue, incongruent and no cue, blank and congruent, blank and incongruent. Moreover, congruent and incongruent trials were combined and this combination paired with blank and no cue conditions. The pairs were analyzed to determine the brain regions that were capable of decoding different conditions (Table 3.3). Similar to the GLM analysis, the pairs that did not contain blank condition did not show any significant results ($p > 0.05$, FWE-corrected, $k = 5$ for all). On the other hand,

the pairs that contrast blank condition with congruent (Figure 3.3), incongruent (Figure 3.4) and the combination of congruent and incongruent (Figure 3.5) ($p < 0.05$, FWE-corrected, $k = 5$ for all)

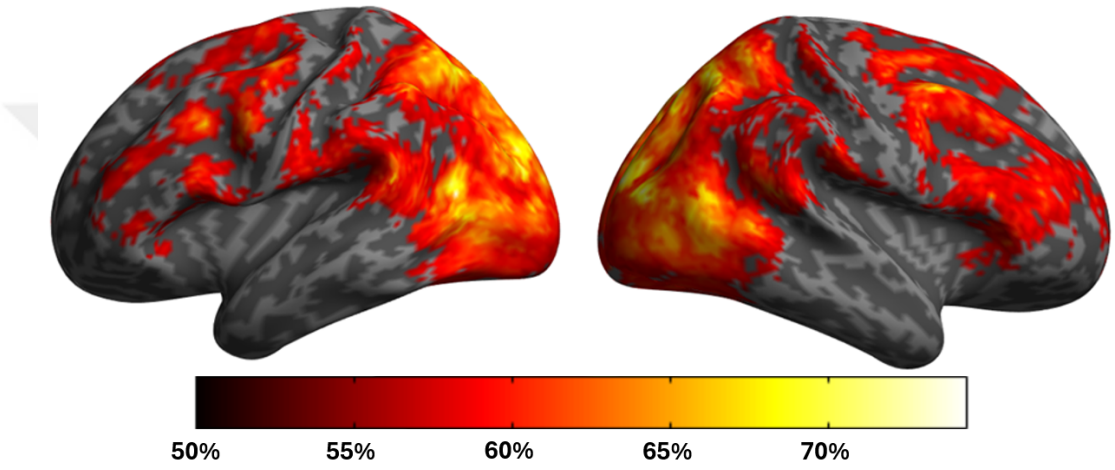

Figure 3.3: MVPA results describing the contrast between congruent and blank trials, with color scale representing classification accuracy.

$$Note : p < 0.05, FWE - corrected, k = 5$$

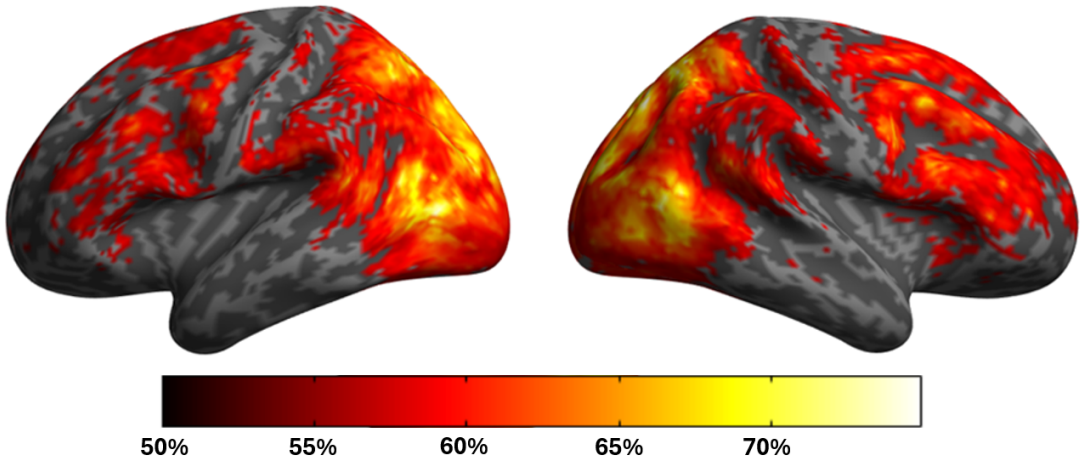

Figure 3.4: MVPA results describing the contrast between incongruent and blank trials, with color scale representing classification accuracy.

$$Note : p < 0.05, FWE - corrected, k = 5$$

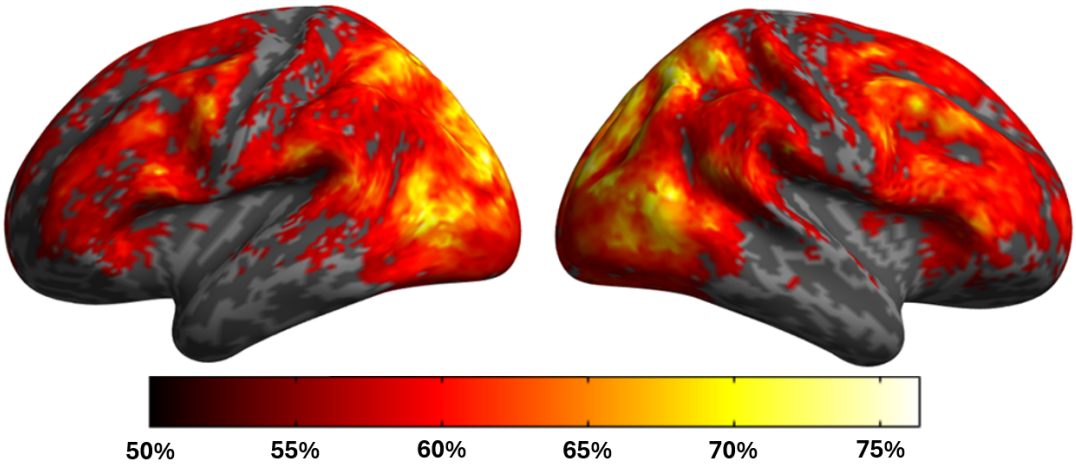

Figure 3.5: MVPA results describing the contrast between combination of congruent+incongruent and blank trials, with color scale representing classification accuracy.

$$Note : p < 0.05, FWE - corrected, k = 5$$

Table 3.3: MVPA Local Maxima Values

	MVPA Results					
	Left			Right		
	Congruent	Incongruent	Congruent+ Incongruent	Congrue nt	Incongruent	Congruent+ Incongruent
PPC				x=24 y=-72 z=56	x=20 y=-76 z=54	x=20 y=-76 z=54
MSFG	x=-6 y=50 z=6			x=2 y=68 z=6		
Caudate	x=-10 y=18 z=-4					
Thalamus Proper		x=-4 y=-0 z=-8	x=-6 y=-24 z=14		x=12 y=6 z=6	
MFG		x=-34 y=54 z=-4				
PCgG					x=2 y=-42 z=4	
FuG			x=-30 y=-40 z=-16			

3.3.1 DCM Model Selection

The models specified in the methods section were created for each of the 8 individual runs for each subject. Bayesian model selection method was applied to these models. The results have shown that the first family was the winning family. This family was selected as the winning family with an expected probability of 67.67% and with an exceedance probability of 100%. Among the families in the first family, the first model was the winning model. The first model stated that both feedforward and feedback connections were present between both of the ROI pairs (pSTS-PPC and PPC-IFG). Moreover, it also states that the connections were modulated by all three of the conditions (congruent, incongruent and no cue) (Figure 3.3.1 and Table 3.4). This model was selected as the most probable model with an expected probability of 63.34% and with an exceedance probability

of 99.98%.

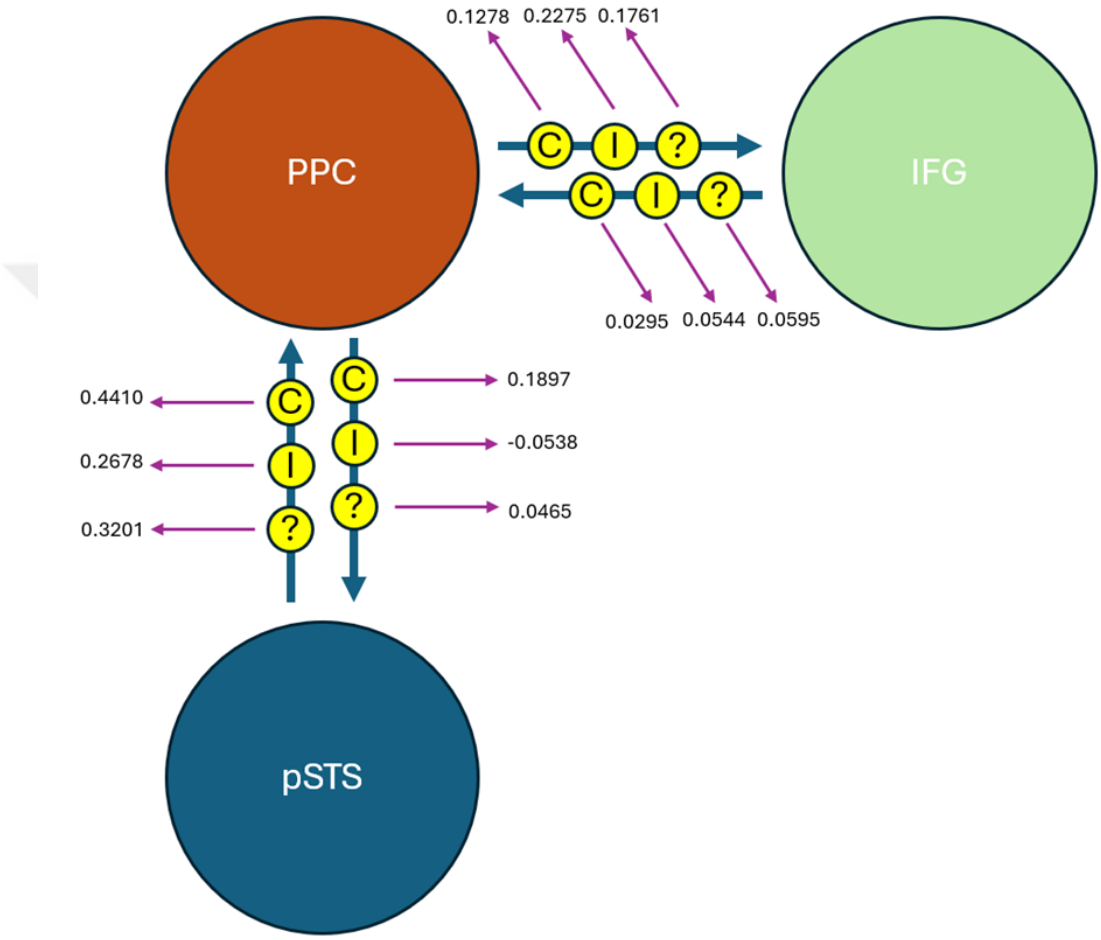

Figure 3.6: The winning model. Note: Modulatory connections of the model can be seen on the figure.

Table 3.4: Winning Model's Endogenous Connections

		From		
		IFG	PPC	pSTS
To	IFG	-0.1208	0.1329	-
	PPC	0.0243	-0.1462	0.1710
	pSTS	-	0.1466	-0.1939

Chapter 4

Discussion

The biological motion literature shows that the speed, accuracy, and efficiency of biological motion perception have led researchers to create models that emphasize its bottom-up processing [1, 31]. According to these models, multiple low-level visual information (e.g., direction of motion, type of action, form of the actor, etc.) are carried to higher perceptual areas by feedforward connections. The integration of this information allows the perception of biological motion [1, 31]. Giese and Poggio [31] also argue that, albeit not essential for perception, top-down processes may facilitate biological motion perception in difficult tasks. Although these models are able to explain biological motion perception in experimental settings, observation of biological motion in nature occurs in significantly more noisy and ambiguous scenarios compared to lab environments. This belief has led researchers to show the essential role of top-down processes for the perception of biological motion [33, 34, 35, 37, 38, 39, 44, 74, 75]. However, the role of expectation in biological motion perception has not yet been thoroughly investigated. Therefore, the primary objective of this study was to challenge the bottom-up models of biological motion perception by showing the role of expectations and predictive processing. To this end, an fMRI study was conducted during which the participants were shown a cue followed by a point-light display that was either congruent or incongruent with the cue.

4.1 Behavioral Results

Inside the scanner, the participants were asked to report the location of the biological motion (left or right). Their behavioral responses were recorded in terms of reaction time and accuracy.

4.1.1 Violation of Expectations Causes a Decrease In Accuracy Scores

In terms of accuracy, two significant conclusions can be drawn: Firstly, the participants were significantly more accurate during no cue condition compared to incongruent condition. Secondly, accuracy in congruent condition did not significantly differ from incongruent condition nor from no cue conditions. In other words, the accuracy results state that misinformation about the stimulus hinders the performance of the participants. Previous studies in the literature also support this statement, arguing that incongruent cues impair the perception of the stimulus [76, 77, 78]. For the current study, it should be acknowledged that the cue is not directly relevant to the task: the task of the participants was not to decide what the biological motion was but to decide where it was. Nevertheless, an incongruent cue about the type of biological motion seems to be enough to reduce the accuracy scores. Therefore, this effect of the cue on the accuracy scores aligns with the findings that biological motion perception includes top-down processes.

4.1.2 Meeting Expectations Allows Faster Processing of Biological Motion

In terms of reaction time results, the participants were significantly faster during congruent condition compared to other conditions. Moreover, no difference in reaction time was observed between incongruent and no cue conditions. Following the aforementioned argument about the relevancy of the cue to the task, and in line with the accuracy results, these differences in reaction time also show the role of top-down processes in biological motion perception. Overall, behavioral results argue that congruent prior information seems to quicken the processing of

biological motion, resulting in faster reaction times, whereas a wrong cue or lack of a cue results in slower reaction times. Facilitation of processing by congruent visual or auditory cues has been supported by multiple previous studies [48, 49, 50, 57, 58, 79, 80, 81]. Although behavioral results support previous literature and the hypothesis of the study by showing an enhanced processing of biological motion during congruent condition, the differences between accuracy and reaction time results should be further discussed. Accuracy findings showed a difference between incongruent and no cue conditions. On the other hand, reaction time results indicated differences between congruent and no cue conditions as well as between congruent and incongruent conditions. In other words, although no cue condition was more accurate than incongruent condition, it did not turn out to be faster. Similarly, although congruent condition led to quicker responses than no cue condition, it was not more accurate. However, these differences between accuracy and reaction time results were expected and they can be explained by the phenomenon called speed-accuracy trade-off [82, 83, 84]. This phenomenon represents the tendency to favor either reaction speed or accuracy at the expense of the other [84]. Moreover, the speed-accuracy trade-off argues that if the participants have enough time, accuracy difference between conditions should be minimized [85]. In the current study, the participants were instructed to prioritize accuracy rather than speed. To ensure this, they were provided with a longer response period (2 seconds) than the average reaction time (0.6 seconds). Thus, before conducting the analyses, behavioral differences between conditions had been anticipated to be observed in the reaction time results rather than accuracy results. In line with this expectation, reaction time results showed significant differences that support the hypothesis of the study. On the other hand, although no significant differences had been expected, accuracy results were still able to indicate a hindrance of processing during incongruent condition as well, which strongly supports the hypothesis of the study.

4.2 Brain Imaging Results

4.2.1 A Strong Activation in the Action Observation Network

The fMRI results of the experiment were analyzed by GLM and MVPA methods. 14 contrasts were created for GLM and 7 contrasts were created for MVPA by pairing regressors of interest (please see sections 3.2 and 3.3 for detailed information about created contrasts). The FWE-corrected GLM results failed to show significant activation except congruent-blank, incongruent-blank, and (congruent+incongruent)-blank contrasts. Significant but weak activations were present in all 3 of these contrasts at right PPC and right IFG. This result supports the previous literature as PPC and IFG are parts of the action observation network. The network consists of pSTS, PPC, and IFG; the areas that consistently engage in the observation of biological motions [4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14].

The FWE-corrected MVPA results were in line with, but substantially stronger than, GLM results. Once again, the contrasts except congruent-blank, incongruent-blank, and (congruent+incongruent)-blank pairings failed to show a significant result. However, all three of these contrasts significantly and strongly showed that the occipital cortex, pSTS, PPC, and IFG were able to decode these conditions. Among these conditions, the right PPC consistently showed local maxima in all three conditions. Ultimately, GLM and MVPA results strongly supported the literature by showing significant activation in essential parts of the action observation network. Additionally, local maxima were observed in the fusiform gyrus in (congruent+incongruent)-blank contrast, providing strong evidence towards the region's biological motion selectivity [15].

An interesting finding in GLM and MVPA results is the observed strong activations in the prefrontal cortex and striatum. Each of the contrasts mentioned above compares trials that require both biological motion perception and decision making with trials that require neither. Since the prefrontal cortex plays a crucial role in both biological motion perception (more specifically, IFG) and

decision making, a difference in its activation among these conditions was expected [4, 5, 6, 7, 12, 13, 51, 86, 87]. Nevertheless, an activation as strong as the results show with multiple local maxima was not anticipated. This raised the possibility of another process playing a role in the results. Another crucial role of the prefrontal cortex happens to be the creation of predictions and prediction errors [51, 88]. Therefore, the results argue that blank conditions might cause the creation of prediction errors. Another finding of the study that proposes strong evidence towards this idea is the local maxima observed in the striatum. Striatum is another indispensable area for the creation of prediction errors [89, 90, 53]. In fact, although it had not been originally intended for, the creation of prediction errors in blank trials is completely reasonable. During blank conditions, the participants expected to see a biological motion stimulus and their expectation was violated. Moreover, the blank trials were infrequent enough (16.67% of the trials) for the participants to reliably expect to see a stimulus. Thus, it appears that the study achieved to create an even stronger, second expectation: The expectation of seeing a biological motion stimulus in each trial. Unfortunately, this expectation falls outside the scope of the present study as it is task-relevant, unlike the task-irrelevant expectations created by the cue. Nevertheless, the study has successfully supported the prediction literature by showing the strong activation of the striatum and prefrontal cortex. It also further contributed to the literature by showing a high-level, socially important stimulus is capable of creating predictions and prediction error signals in the prefrontal cortex and striatum.

Although these results succeeded at supporting the current literature, they failed at supporting the hypothesis of the study. A significant difference was not observed between congruent and incongruent conditions by GLM analysis nor by MVPA. A lack of difference among congruent, incongruent, and no cue conditions is supported by previous EEG experiments on prior information [58, 91, 92]. Nevertheless, according to the previous fMRI literature and the behavioral results of the current study, an activation was expected to be observed between those two conditions [49, 93]. It is believed that this lack of difference is due to the primary limitation of the study: A low number of trials caused by the 75%

congruency nature of the study. This limitation will be further discussed in section 4.4. Alternatively, a second potential explanation for the lack of a significant difference between congruent and incongruent conditions can be the type of stimuli used. During the experiment, point-light displays of a walking and a kicking human were used. However, previous brain imaging studies state that activation of STS is significantly lower while observing point-light displays compared to the observation of naturalistic videos [36, 94]. This finding provides empirical evidence for the weaker activation of pSTS compared to pSTS in the current MVPA results. Moreover, Jastorff and colleagues [95] have successfully shown that the presentation of 3D biological motions to participants elicits a stronger activation in the action observation network compared to the presentation of 2D biological motions. Thus, it is highly likely that the utilization of a video-taped biological motion would result in a stronger activation, potentially resulting in a significant difference in congruent-incongruent condition. Nevertheless, it is still believed that the utilization of traditional 2D point-light displays was the right choice for an initial study in the field as they allowed the control of possible confounding factors.

4.2.2 The Winning Model: Every Feedforward and Feedback Connection Is Present

In order to investigate the connections within the action observation network, DCM analysis was conducted on the fMRI data. In light of the current literature, 64 possible models were created with different feedback connections. A clear winning model was selected by the Bayesian Model Selection procedure. The winning model argues that information first enters pSTS, which is followed by feedforward and feedback connections between pSTS-PPC and PPC-IFG during all three of the stimulus conditions. This model contributes to the biological motion literature by arguing that biological motion processing is not solely a bottom-up process. There exist feedback connections and top-down processes during biological motion processing. More specifically, feedback connections are present whether prior information is given or not, and whether the given prior information is correct or incorrect. The model also shows that these feedback

connections are weaker than feedforward connections. Moreover, the incongruent feedback connection between pSTS and PPC has a negative strength, stating that incongruent condition results in an inhibitory or regulating signal. This effect of incongruent stimuli is supported by previous predictions studies and builds on them by using socially meaningful stimuli [46, 49]. The DCM analysis also further contributes to the literature by being the first study that creates a prior information model for biological motion perception. Moreover, besides these contributions to the literature, the model also supports previous biological motion studies by showing a clear feedforward flow of information from pSTS to PPC and from PPC to IFG [6, 7, 8].

4.3 General Discussion

Ultimately, the study greatly contributed to and supported biological motion perception and prediction literatures by combining these two literatures. Firstly, the results supported the biological motion literature by clearly showing activation of the action observation network (as well as the fusiform gyrus) while a biological motion is observed. Secondly, the expectation violation during blank trials supported the expectation literature by showing a strong activation of the striatum and prefrontal cortex. Thirdly, the results contributed to the literature by building on the findings that biological motion processing requires top-down processes. The results support this idea by showing the significant effect of predictive coding on the performance of the participants. Fourthly, by selecting a winning model among 64 possible ones, the study creates a new model for biological motion perception that shows how the flow of information is affected by predictive coding. Lastly, the winning model also proposes significant evidence towards the idea that top-down processes and feedback information are required for biological motion perception since the feedback connections are still present during the control condition.

4.4 Limitations of the Study

Although the findings of the current study are supported by various analysis methods, it should be acknowledged that some limitations exist for this study. Firstly and most importantly, as mentioned before, the study suffers from a low number of trials because of its 75% congruency nature. As a result, incongruent, no cue, and blank conditions each had 3 times fewer trials than congruent condition. Consequently, this also caused weak MVPA results as 1/3 of congruent trials were chosen for this analysis in order to have an equal number of trials across conditions. The lack of difference in the congruent-incongruent contrast for GLM and MVPA analyses is believed to be caused by this limitation. Although it was possible to account for this limitation by increasing the number of trials for incongruent trials, this would significantly prolong the duration of the study. In order to preserve the trial ratios among conditions, each new incongruent trial would result in the addition of 6 trials in total (61 to 73 seconds of experiment duration). Therefore, aiming for a high number of incongruent trials would cause the study to be impractically long for an fMRI experiment, even in the span of multiple sessions. Moreover, such a long duration for the current paradigm is expected to cause significant learning effects.

A second limitation of the study can be argued to be a relatively low generalizability of the results caused by the lack of variation in selected actions. The current study only utilized two unique actions. The main reason for choosing a walking and a kicking man is that walking and kicking seem to be among the easiest point-light displays to recognize, while also being distinct enough to discriminate between them. However, this choice raises the question of whether the results would differ if a higher number of unique actions or different actions were used. Different action types have been shown to be processed uniquely in PPC [96]. Thus, using communicative actions (such as waving), using a female PLD, or a PLD with emotion might be expected to result in different findings. Moreover, the display type is another factor that limits the generalizability of the experiment. Instead of using 2D point-light displays, videos of real-life actors performing the actions can significantly increase the strength of the results while also better reflecting daily life scenarios [36, 94, 95]. Therefore, although the

aim of the study is to understand the underlying neural mechanisms of biological motion perception in a controlled setting, it can be argued that the findings do not reflect exact daily life scenarios.

4.5 Future Directions

The study contributes to the literature not only with its findings but also by providing a solid basis for multiple future studies. First of all, future studies can replicate the current experiment with different display types, action types, or different cues in order to increase the generalizability of the findings. Real-life videos (instead of PLDs), communicative actions, PLDs with emotions, female PLDs, or any combination of these manipulations can be used to build on the current experiment. In a recent study, Elmas and his colleagues (2023) showed that giving prior information about the gender or emotion of the PLD failed to have a significant behavioral effect on participants. However, choosing different cue-stimuli pairs and investigating neural responses might still be worth exploring. Moreover, multiple fMRI studies with different modifications can be conducted based on the current study to gain a deeper understanding of the neural mechanisms underlying biological motion perception. For instance, experiments in which the congruency rate is different from 75%, or in which the cue gives different prior information (such as the position of biological motion) can be investigated.

4.6 Conclusion

In conclusion, the current study has contributed to the literature by being the first that provides a model to explain the role of prior information in biological motion perception. The findings of the study clearly argue that biological motion perception is a high-level cognitive function. They also show significant evidence towards the presence of top-down processes and feedback connections, challenging the view that biological motion perception is solely a bottom-up process.

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