# EFFECTIVE CONNECTIVITY IN CORTICAL REGIONS DURING BOTTOM-UP PERCEPTION OF BIOLOGICAL MOTION UNDER ATTENTIONAL LOAD: AN FMRI-DCM STUDY

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Sezan Mert

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Effective connectivity in cortical regions during bottom-up perception of biological motion under attentional load: An fMRI-DCM study
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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

# EFFECTIVE CONNECTIVITY IN CORTICAL REGIONS DURING BOTTOM-UP PERCEPTION OF BIOLOGICAL MOTION UNDER ATTENTIONAL LOAD: AN FMRI-DCM STUDY

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July 2024

The ability to detect biological motion holds an evolutionarily important role in vital and social functions. However, in our daily lives, we perceive biological motion while we are at a task most of the time. In other words, it is perceived when our attention is directed at another thing. In this aspect, understanding the dynamics of its bottom-up perception is of high importance. Meanwhile, the attentional mechanisms and where their effects occur are a matter of debate in the literature, sparking off various theories, such as early selection, late selection, and attentional load theory. Dynamic causal modeling (DCM) is a suitable tool for investigating the dynamics of attentional effects on the network, enabling the bottom-up perception of biological motion, and comparing the existing theories in the literature with Bayesian graph models. To this end, we utilized the DCM approach with fMRI data collected using an attentional load paradigm and biological motion peripheral distractors [1]. In our model space, we modeled the theories of selective attention along with two complementary models. The Bayesian Model Selection (BMS) showed that the model that explained the data the best was the model where both attentional load conditions modulated all top-down connections rather than the models of existing theories. This showed that attentional effects take part in the bottom-up perception, not in a focused location, such as early or late, but in a more distributed manner throughout the processing pipeline. Further statistical tests on the model parameters yielded no difference between load conditions and between biological motion and scrambled motion in their modulation strengths. Yet, the strengths of biological motion on different connections were different from each other. A similar observation is also made for the low load condition but not for the scrambled motion and high load

conditions. The former can be accepted as evidence for the differential processing of biological and scrambled motion. The latter may be explained by a spillover of perceptual resources on biological motion and causing competition in low-load conditions.



*Keywords:* Biological motion, selective attention, early selection, late selection, attentional load, fMRI, DCM.

# ÖZET

# BİYOLOJİK HAREKETİN DİKKAT YÜKÜ ALTINDA YUKARIDAN AŞAĞI İŞLENMESİNDEKİ KORTİKAL BÖLGELERİN ETKİN BAĞLANIRLIĞI: BİR İMRG-DNM ÇALIŞMASI

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

Biyolojik hareketi tespit edebilme yetisi yaşamsal ve sosyal işlevler için evrimsel olarak önemli bir role sahiptir. Fakat, günlük yaşamlarımızda bizler biyolojik hareketi genellikle bir iş üzerindeyken algılarız. Diğer bir deyişle, biyolojik hareket dikkatimiz başka bir yerde iken algılanır. Bu açıdan, biyolojik hareketin aşağıdan yukarıya işlenmesindeki dinamikleri anlamak önem arz eder. Bununla birlikte, dikkat mekanizmaları ve dikkatin etkilerinin nerede gerçekleştiği alanyazında, erken seçilim, geç seçilim ve dikkat yükü teorisi gibi farklı teorilere yol açmış bir tartışma konusudur. Dinamik nedensel modelleme (DNM), yukarıdan aşağıya biyolojik hareket algısını sağlayan ağın üzerindeki dikkat yükü etkilerinin dinamiğini incelemek için ve alanyazında var olan teorileri karşılaştırmak için uygun bir araçtır. Bu nedenle, biz, dikkat yükü paradigmasını ve çevrel biyolojik hareket çeldiricelerini kullanan bir işlevsel manyetik rezonans görüntüleme (iMRG) deneyi ile birlikte DNM yaklaşımını kullandık [1]. Model uzayımıza seçici dikkat teorilerini modelleyen modellerin yanı sıra tamamlayıcı iki model de dahil ettik. Bayesyen Model Seçimi (BMS), verileri en iyi açıklayan modelin, mevcut teorilerin modellerinden ziyade, her iki dikkat yükü koşulunun da tüm yukarıdan aşağıya bağlantıları modüle ettiği model olduğunu gösterdi. Bu da alanyazında var olan mevcut teorilerin savunduğu, odaklanmış, erken veya geç bir seçilimden ziyade işleme hattı boyunca yayılmış dikkat etkilerinin olduğunu gösterdi. Model parametreleri üzerinde yapılan ek istatistiksel testler, yük koşulları arasında ve biyolojik hareket ile karıştırılmış hareket arasında modülasyon güçlerinde hiçbir fark olmadığını ortaya koydu. Buna rağmen biyolojik hareketin farklı bağlantılar üzerindeki modülasyonları birbirinden farklıydı. Benzer bir gözlem düşük yük koşulu için de yapılırken, karıştırılmış biyolojik hareket uyaranı veya yüksek

dikkat yükü koşulu için yapılmadı. İlk bulgu, biyolojik hareket ve karıştırılmış biyolojik hareketin farklı işlenmesi için bir kanıt sağlamaktadır. İkinci bulgu ise düşük dikkat yükünde algısal kapasitenin biyolojik hareket uyaranına taşması ve bunun bir rekabet oluşturması ile açıklanabilir.

*Anahtar sözcükler*: Biyolojik hareket, seçici dikkat, erken seçilim, geç seçilim, iMRG, DNM.

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# Contents

# List of Figures

# List of Tables

# Chapter 1

# Introduction

Imagine driving and entering a junction with many cars. Suddenly, a pedestrian steps into the road. Taking the action of hitting the brakes requires the recognition of the pedestrian. Although this occurs in milliseconds, coordination and cooperation of various regions in the brain are needed. Now, imagine that at the same time, your child in the back seat starts to cry, and your phone rings. Would you still be able to detect the pedestrian?

In our daily lives, we are exposed to many stimuli; not all of them are as significant as the others. So, in our perceptual processing pipeline, we need to be selecting the ones that are relevant to us. However, how this selection occurs, where it happens, and if it is the same for tasks with different difficulties is a debate that still goes on in the literature.

Understanding the network and its functions that enable biological motion perception under attentional load conditions is essential for a better understanding of the brain. Furthermore, it may help regulate safety measures related to the scenario in the first paragraph or may be beneficial in formulating a treatment for attention deficit patients.

Attention is defined as the process of focusing on some entities while ignoring others [2]. Various aspects, functions, and related concepts of attention are

defined in the literature, such as divided attention, overt or covert attention, sustained attention, and selective attention. Readers may refer to this source for more detailed definitions of these concepts [3]. Here, in this thesis, we will focus on selective attention, and the word "attention" will be used to refer to selective attention in the thesis.

The following sections will provide background on biological motion and neural correlates of its perception, as well as attentional networks in the brain and discussions in the literature on the locus of attention.

## 1.1 Biological Motion

In their pioneering work, Johansson operationalized the term "biological motion" (BM) as "motion patterns in animals and men" [4]. From an evolutionary point of view, the ability to perceive the motion of living beings serves a vital role in discriminating prey from predators [5]. Likewise, for the social relations of animals that adopt a communal life, such as humans, biological motion is especially valuable for communication and establishing relations [6].

Biological motion perception is conventionally studied in the literature with point-light displays (PLD). These stimuli are first proposed by Johansson and obtained by recording the actions of an actor in the dark on whose joints placed some light sources [4] as shown in Figure 1.1. In this way, the motion is extracted, leaving out the other irrelevant features behind, such as the color, texture, and contrasts belonging to the actor or the background. It is noted that this abstracted motion of dots is still perceived as a person performing these actions to an extent where the subjects can recognize the mood and the gender of the actor [7]. These stimuli are also preferred as they provide flexibility in manipulation. For instance, adding some irrelevant moving dots can be used to introduce noise to the stimuli for decision-making experiments [8], or the locations of the dots can be shuffled to obtain a control stimulus that does not resemble BM but

has the same motion trajectories [1]. In recent times, researchers can find various PLD datasets offering a wide variety of action and actor types thanks to the advancements in motion capture (MoCap) technology [9].

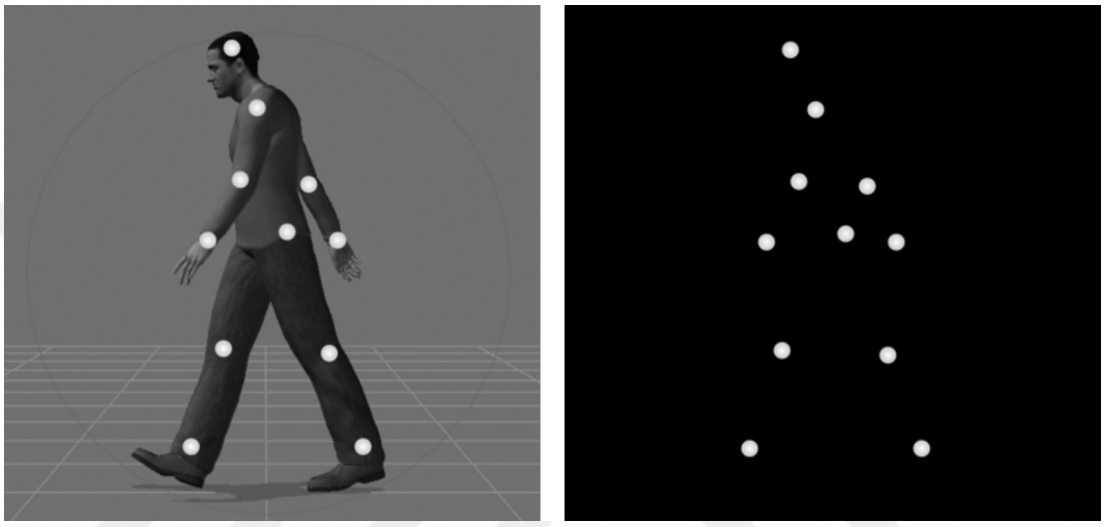


Figure 1.1: Process of obtaining the point light display for the biological motion stimulus. Reprinted from [10] with permission.

### 1.1.1 Neural Basis of Biological Motion Perception

In humans and non-human primates, the brain areas and the network that facilitates biological motion perception have been identified mostly with a vast array of neuroimaging (functional magnetic resonance imaging (fMRI) and electroencephalography (EEG)) [11–18] and electrophysiology studies [19–21]. These regions enable the steps of the biological motion perception process that Thompson and Parasuraman define as (i) perception of features that characterize an action, (ii) fusion of these features into the representation of the action, and (iii) identification of intention of the action using the context and cues in the environment [22].

For biological motion perception, form and motion features are crucial. Thus, the two-pathway processing framework also applies to the perception of biological motion [23]. According to this, two pathways originate from the early visual cortex, V1, one mainly processing the form features called the ventral pathway,

and the other primarily processing the motion features called the dorsal pathway. The processing of action-specific features is shown to begin at the extrastriate cortex and ascending limb of the posterior inferior temporal sulcus (pITS). More specifically, the extrastriate body area (EBA), a body part sensitive region, and the area middle temporal complex (MT+), which was reported to show increased activity for biological motion rather than the scrambled motion, are thought to be involved in the processing of biological motion features [11, 13, 22, 24].

In the second processing step, feature integration is thought to happen in the superior temporal sulcus (STS), supported by transcranial magnetic stimulation (TMS) [25,26], lesion [12], and fMRI studies [22,27–32]. Moreover, although there are interactions between the ventral and dorsal pathways, monkey electrophysiology data suggests that these two pathways converge at STS [33]. Hence, it is viewed as an integration hub, and it can be said that this is a higher-level processing region than the aforementioned action-specific areas. A piece of evidence for it being a higher-level region is that STS also shows viewpoint invariance for actions [29, 34].

Understanding the intentions of actions is suggested as the last step of processing biological motion, and this function is thought to be mediated by the inferior parietal and inferior frontal cortex [22]. In particular, the parts of the parietal cortex, the inferior parietal lobule (IPL), and the anterior intraparietal sulcus (aIPS) are shown to be encoding the goals of the observed action [35]. The activations in this region for different action types are studied [36–38]. These studies showed that there are category-selective areas, especially at the posterior parietal cortex [39]. Lately, Urgen and Orban have shown the specialization of areas within the parietal cortex for various action types, such as communicative and object manipulation action [40]. On the other hand, a region at the inferior frontal cortex (IFC), the ventral premotor cortex (vPMC), is thought to primarily play a role in effector-related processing [41, 42]. Another region in the IFC, the inferior frontal gyrus (IFG), encodes the goals of the objects that are informed by the context [43, 44].

Altogether, the literature shows that the coordinated activity of early-level

visual regions, occipitotemporal cortex, and parietal and premotor cortices enable the perception of biological motion. These regions are shown in Figure 1.2.

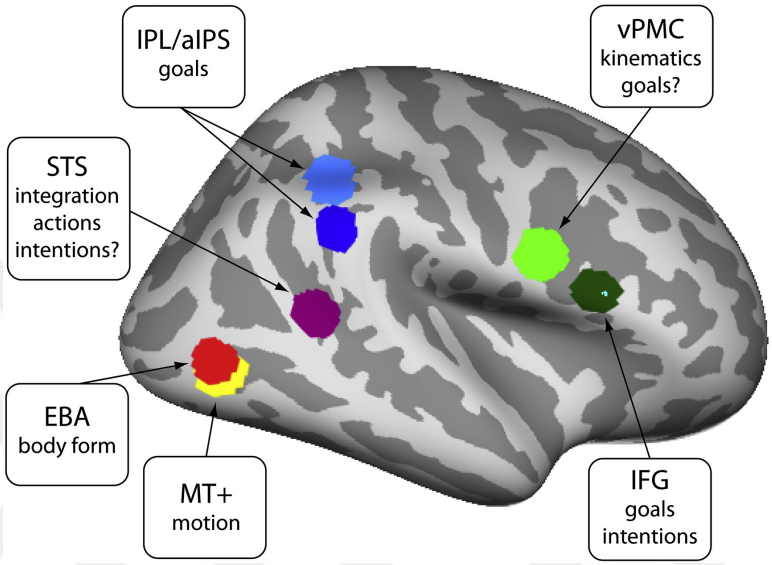



Figure 1.2: The regions associated with action observation. Reprinted from [22] with permission.

## 1.2 Bottom-up and Top-down Processing of Biological Motion

Initially, biological motion is studied with passive viewing or active tasks in the literature. Consequently, the models of biological motion perception were missing any feedback connections or modules that would represent these top-down effects [45–47]. These models are feedforward hierarchical models of ventral and dorsal pathways with the inclusion of STS as a fusion stage of these form and motion features. However, lately, the research started to focus on the attentional effects on the biological motion processes. In fact, a considerable amount of work has accumulated in this area. With their influential work, Thornton and colleagues showed that attention is substantial for biological motion perception, especially when the information in the visual field is more sparse [48].

The following research further established various paradigms to manipulate

the bottom-up versus top-down processing of BM. One such paradigm is the Flanker task [49]. Although it is first defined as a task with letter stimuli, the BM version of this task has three PLDs where the subjects are asked to focus on the BM in the middle. The peripheral PLDs interfered with the performance when their direction was incongruent with the target PLD, thus showing the bottom-up processing of BM [50]. A very similar paradigm is also utilized by Ikeda and colleagues [51]. They altered the distance of the peripheral PLDs to the center, where the attention is directed. They showed that performance is more affected when the flankers are closer and that scrambled flankers do not affect performance, regardless of their distance from the central stimulus.

To understand if the top-down and bottom-up processing of BM has any differences in terms of the neural pathways, several neuroimaging studies have been conducted. The studies that investigated the bottom-up processing of BM utilized a main task that does not involve BM and investigated the regions that were activated when the attentional resources were not allocated to BM. On the other hand, for the top-down processing of BM, the main tasks that involve BM were used so that the attentional resources were allocated to the BM stimulus.

One of the first neuroimaging studies on the top-down processing of BM is conducted by Saygin and colleagues [27]. In this study, the participants performed a task regarding the color of the dots of the BM. They observed activations in the occipitotemporal cortex (OTC), STS, and frontoparietal regions, including the IFG, intraparietal sulcus (IPS), and vPMC. Meanwhile, the studies investigated the bottom-up perception of BM, such as [24] also observed activations in earlier areas up until STS, while they did not find frontal activations. Nizamoglu and Urgen also investigated the bottom-up perception of BM by using a central task [1]. Different from the previous literature on bottom-up BM perception studies, they manipulated the attentional load rather than simply creating a task where attention to the BM is binary. In this work, they showed that during the low-load conditions, OTC activations were prominent; however, when, for the high-load conditions, only early visual cortex activations remained, providing evidence for the modulation of motion-sensitive regions by attentional load.

In the study by Safford et al., the top-down and bottom-up processing were investigated with the same stimuli [52]. Participants attended either the tool motion or the BM, which were both PLDs and overlaid onto each other. As a result of their fMRI analyses, they showed a suppressed STS activation for tool motion (bottom-up perception of BM) compared to BM (top-down perception of BM). Similar work has been done by Saygin and Sereno using a retinotopy study [53]. They showed that top-down perception of BM resulted in retinotopic maps in the lateral occipital cortex (LOC), ventral temporal cortex (VTC), action-feature sensitive areas such as MT+, STS, and IPS, and more attention-related regions such as posterior parietal cortex (PPC) and frontal eye field (FEF). The maps decreased to only OTC and IPS regions when the participants attended the 2-back task in the center rather than the BM.

In summary, these studies showed that the motion-specific features are processed in a bottom-up manner, recruiting the areas such as EBA, FBA, and MT+, while more high-level integration and intention-understanding functions require attentional resources to modulate regions such as STS and frontoparietal regions.

## 1.3 Theories of Attentional Selection Mechanisms

To obtain a holistic view of the effects of attentional mechanisms on biological motion perception, the literature on attention networks and how they act on perceptual processes should be discussed as well. The selective nature of attention started to be studied with auditory modality almost two decades ago before the works of biological motion perception. The first milestone in the selective attention research was the cocktail party problem coined by Cherry in 1953 [54]. In their now classic study, the subjects are listened to two speech recordings simultaneously with each of their ears (dichotic listening) and asked to repeat the speech from only one side. When the participants were asked about the content of speech in the ignored ear, they could not provide an answer [55].

This experimental paradigm was very influential; thus, it was used and extended in many studies that followed (to name some, see [56–59]; please refer to this review for a more comprehensive list of works that use this paradigm [60]). It also led to a debate in the literature about the locus of attention, i.e., at which point of the perceptual process this filtering effect occurs. The following sections will explain the main theories in the literature about the locus of selective attention.

### 1.3.1 Early or Late Selection?

The early selection theories first merged around the late 1950s with Broadbent's filter theory [61]. Using the dichotomic listening paradigm, they suggested that due to the system's limited capacity, there is a bottleneck in the perceptual processes. Due to this limited capacity, information is filtered according to the physical features before being perceived. Hence, this model proposes an early elimination of the stimuli before reaching the later processing stages. Accordingly, with early filtering, cognitive overload is prevented.

Using auditory and visual stimuli, the following research initially found supportive outcomes for this theory [62–66]. For instance, von Wright used a paradigm where the participants were shown brief stimuli consisting of a grid of letters [67]. Subjects were asked to report either all letters (whole report) or letters with certain features for various features (partial report), such as location, color, size, and orientation. As a result, they showed that the selection process is more successful with certain physical features, such as color and location. Hence, they concluded that physical features enable efficient selection.

Then, the early selection theory is challenged by a series of studies [68–72]. One of the studies that stands out is by Moray. In this study, using the dichotomic listening task and adding the subjects' names to the stimulus in the unattended ear, they could show that subjects recognized their names and that unattended information could pass through the suggested "filter" [73]. This provides evidence that the unattended stimuli are processed, at least to some extent. Also, in the

visual modality, the late selection view is supported by the Stroop task [74] and the paradigm used by Eriksen [49]. In the former, the semantic information of the word interferes with the visual information. On the other hand, in the latter, the unattended flanker letters interfere with the task performance related to the attended letter.

### 1.3.2 A Reconciliation: Perceptual Load Theory

While the debate between the early and late selection continued, Kahneman and Triesman pointed out that these two groups of findings stem from the difference between the experimental paradigms employed in their works [75]. They proposed that studies favoring the early selection theory used more complex paradigms than those of the late selection theory supporters. Then, on top of this inspection, Lavie and Tsal built the perceptual load theory as the determinant of the locus of attentional selection [76].

Perceptual load theory combines the assumptions of the early and late selection theories. First, it states that the perceptual capacity is limited, as the early selection theories suggest. However, it also states that the allocation of this perceptual capacity occurs in a mandatory and automatic manner, as the late selection theory supports [77]. The level of attentional selection is, therefore, determined by the main task that is performed. If the main task does not require a high perceptual capacity, the remaining capacity will "spill out" to the distractors. In this case, peripheral distractors will be perceived and eliminated later in the perceptual hierarchy (late selection). On the other hand, when the main task is perceptually demanding, there will be no capacity left to perceive the distractors. As a result, these distractors will not be perceived, which is equivalent to an early selection [78, 79].

Lavie and many researchers provided supportive evidence in their following studies with behavioral and neuroimaging data (see review for an extensive list [80]). In one of the earliest of these studies, Rees and colleagues used two language tasks: low load and high load [81]. In the periphery, they showed participants

moving dots irrelevant to the task in the center. Consequently, they showed that the motion-sensitive area V5 had a higher activation during the low-load task than the high-load task. Similarly, Schwartz et al. showed that the peripheral checkerboard stimulus evoked a higher activation in the primary visual cortex V1 in the low-load condition than in the high-load condition [82]. Significantly, they used the same visual stimulus for both load conditions and manipulated the load only by changing the definition of the task. This paradigm was also used by Nizamoğlu and Ürgen with biological motion peripheral distractors to understand the neural basis of biological motion perception under different attentional load conditions [1]. In this study, their multivariate pattern analysis (MVPA) showed that the decoding accuracy at the motion-sensitive area MT was significantly higher for the low-load condition than the high-load condition.

However, several researchers also challenge perceptual load theory as it lacks a stand-alone definition of perceptual load [83] and due to the physical properties of the stimuli widely used in perceptual load theory research. In particular, the visual search tasks studied with presentations of multiple items in the display were criticized. These experiments manipulated the number of objects in the visual field to alter the perceptual load. For this reason, Tsal and Benoni argued that the increased perceptual load may not be the sole cause of the lower interference by the distractors in the high-load conditions [84]. Instead, they suggest it could be "due to the dilution of the distractor by the presence of the neutral items" in the high-load conditions [83].

To summarize, the locus of attention is an old debate that discusses not only the location of attentional effects but also the mechanism that determines this locus. While the early-level selection proponents suggest that the bottleneck should occur in the very first perpetual stages due to a limited perpetual capacity, the late-selection supporters propose that this perceptual capacity is automatically allocated to the stimuli and the elimination occurs at a higher level region of the perceptual processing pipeline. Perceptual load theory adopts the view of the limited perceptual capacity of early selection and the automated allocation of this perceptual capacity of late selection. It suggests, as a result, the elimination depends on the perceptual load of the main task: if it uses up all the perceptual

capacity, then the elimination occurs early due to the lack of perceptual capacity; if there is perceptual capacity left, then it will be automatically used by the peripheral distractors which will be eliminated later on.

## 1.4 Neural Basis of Visual Attentional Control

Understanding the brain areas that facilitate attentional control is crucial for unraveling the effects of attention on biological motion perception and relating the regions, enabling these bottom-up and top-down processes through effective connectivity.

Visuospatial attention can be driven by internal (endogenous) or external (exogenous) factors. These are also named top-down and bottom-up selection, respectively [85]. To exemplify, attention can be directed at a certain place due to its salience (exogenous) or due to its relevance (endogenous) to the performed task. Neuroimaging studies pointed out two main visuospatial attentional networks in the brain that mediate the control of attention as a result of the interplay of their activations [86]. These are known as the ventral attention network (VAN) and dorsal attention network (DAN). The VAN consists of the regions of the ventral frontal cortex (VFC) and temporoparietal junction (TPJ), while IPS, superior parietal lobule (SPL), and FEF regions are thought to be the core regions in DAN, as shown in Figure 1.3 [87]. Initially, DAN and VAN are proposed as the pathways that facilitated the top-down and bottom-up selectivity, respectively [85]. However, the ensuing studies showed that this correspondence is not that straightforward [86]. Instead, it is suggested that the VAN is suppressed and DAN is activated when the attention is directed to a stimulus, regardless of whether it is an endogenous or exogenous driver. Yet, when the attention is reoriented, both the VAN and DAN activation are increased. Reorientation of attention is defined as the "adjustments in response to a novel or unexpected stimulus" by Corbetta et al. [88].

Aside from these two regions, it is reported that the default mode network

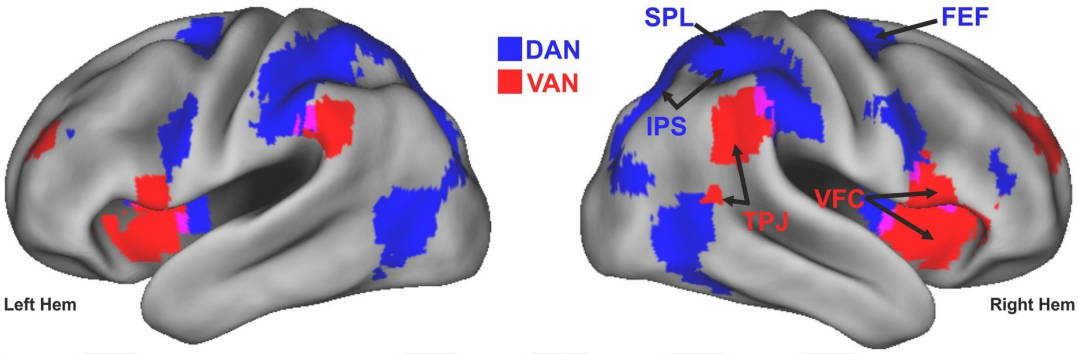



Figure 1.3: The regions associated with visuospatial attention. Adapted from [86], CC BY 4.0.

(DMN), a network consisting of the medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), and precuneus, shows increased activation in the resting state when the attention is directed internally and inactivated in the presence of stimuli or task conditions [89, 90]. Supporting this, Nizamoglu and Urgen also showed, with their univariate analysis results, that DMN activity has decreased with the increased attentional load of the task [1].

Overall, attentional control is enabled through the interplay of three main networks: DAN, VAN, and DMN. While DAN is activated more with directed attention, and VAN is activated with unexpected stimuli. DMN is proposed as a network that is activated more with an idle, roaming mind, working antagonistically with the DAN.

## 1.5 Attention, Biological Motion and Effective Connectivity

Dynamic models provide convenient tools for modeling the effects of attention on networks of cognitive processes and understanding the connections between attention networks and perceptual networks since attention is a temporally changing, top-down process. Therefore, dynamic models, such as dynamic causal

modeling (DCM), are widely used for revealing attentional effects on visual perception [89]. Although BM perception is also a dynamic process that involves various regions, the number of effective connectivity studies that investigate BM is rather rare. Moreover, to the best of our knowledge, no connectivity studies have investigated the relationship between BM processes and attentional load. The following sections will focus on the literature on connectivity for BM and attention.

### 1.5.1 Biological Motion and Effective Connectivity

There are only a few connectivity studies in the literature regarding the processing of BM with PLDs. Interestingly, these studies are mainly concerned with cerebro-cerebellar connectivity in the process of action perception [91,92]. In one of these studies, they used point-light BM stimuli with superposed noise dots with high angular resolution diffusion imaging (HARDI) and fMRI for DCM [91]. The task was to determine the presence of a walker; hence, it is a top-down BM processing task. They identified their regions of interest (ROIs) as the early visual cortex (occipital cortex), middle temporal cortex (MT), fusiform gyrus (FFG), STS, right anterior insula (INS), right inferior frontal gyrus (IFG), and left lateral cerebellar lobule Crus I (LCB). They used three different model spaces with combinations of these ROIs: temporal module (MT, STS, and FFG), temporal module's connections to the insula, and IFG (MT, STS, FFG, INS, and IFG), and top-down connections to the early visual cortex (OCC, STS, INS, and IFG). In these models, BM modulated the intrinsic connectivities in these networks. Their results supported that STS is an integrator region that provides little to no feedback to MT and FFG, that STS is not a "gatekeeper" region between the action-feature processing regions (MT and FFG) and the frontal areas (IFG and insula) and that early visual cortex receives BM-specific excitatory influences from insula while it receives inhibitory feedback from IFG.

In another study that utilizes PLDs, two tasks were assigned to the participants, half of whom are adults with autism spectrum disorders (ASD) [93]. In one

task, participants discriminated between BM and SCR motion from noisy stimuli, and in the other task, they were asked to perform a color discrimination task related to one of the dots of the PLD. This way, they investigated the top-down and bottom-up perception of BM and effective connectivity in the right STS and mPFC. Different from the previous studies, they used the psycho-physiological interactions (PPI) method. Unlike DCM, PPI is used to understand the connectivity of a seed region with another region through regression [94]. Here, they found that the right STS-mPFC coupling was higher for ASD compared to healthy participants during the top-down BM perception, and there was no significant difference in coupling between ASD and healthy participants.

### 1.5.2 Attention and Effective Connectivity

In one of the early works on effective connectivity, Büchel and Friston utilized moving dot stimuli and investigated the effective connectivities between early visual cortex V1, motion-sensitive region V5, and attention-related area PPC by using structural equation model [95]. Later, in his canonical DCM study, Friston et al. applied DCM to this data [96]. In this DCM version, on top of the V1, V5, and superior posterior parietal cortex (sPPC), they also add the IFG. In this network, the connection from V1 to V5 is modulated by motion, and connections from sPPC to V5 and from IFG to sPPC are modulated by the attention condition. As this was the first work that DCM proposed for fMRI, they did not use other models or Bayesian model comparison.

A more recent study explores the effects of task demand in a moving dots decision-making paradigm using both EEG and fMRI data combined with DCM analysis [97]. Their models are constructed with regions V1, V5, FEF, and mPFC, and their model space consists of models that have the same intrinsic connection between these regions while the task demand modulates different connections. Their results showed that task demands modulated the bi-directional intrinsic connections between V1 and V5.

Another work by Bowling, Friston, and Hopfinger utilizes DCM to model the

directionality of connections between the frontal and parietal areas for a better understanding of top-down versus bottom-up attentional mechanisms [98]. In this, they used three types of cues that were (1) endogenous: indicating the likely side of stimulus appereance with color of fixation, (2) exogenous: cue provided by a white square showing the location of incoming stimulus correctly 50% of the time, or (3) anti-predictive exogenous: cue provided by a white square indicating the location of incoming stimulus correctly 83% of the time. They showed that endogenous and exogenous attention conditions modulate the frontoparietal connections distinctively.

There are also works in the literature that model the effects of attentional load on visual networks. An fMRI-DCM study used a very similar paradigm to that of Schwartz's [82] with peripheral color stimuli to investigate the differences in the effects of attentional load on the connectivity between V1, V4, and IPS between the healthy subjects and depression patients [99]. As a result, they found out that the model that explains the connectivity for the healthy subjects included a high attentional load effect on the IPS, which in turn suppressed the V4 activation, while the patient population's best model had modulatory effects of both low-load and high-load conditions on the IPS.

In short, the BM perception and attention are investigated in a separate fashion within the effective connectivity framework. While the BM studies with PLDs mostly focused on the connectivity of the cerebro-cerebellar network, the attentional studies mostly utilized motion stimuli with moving dots. Therefore, the need to aggregate these two separate lines of work is evident.

## 1.6 Current Study

In the literature, different hypotheses are proposed on the loci of attentional selectivity. Furthermore, various works have been done on the effects of attention on the connectivity of networks of visual perception. These works used static images and motion stimuli such as moving dots or BM. Nevertheless, these studies

that used BM only used paradigms that elicited a top-down perception of BM, and they did not provide information about connectivity for the bottom-up perception of BM. Moreover, to the best of our knowledge, there are no studies with BM that alter attentional load in their tasks. There are, however, studies that used attentional load, yet they did not use peripheral distractors or investigate how effective connectivity of the network that processes this peripheral stimulus is modulated by the attentional load. Therefore, in this thesis, our aim is to understand the effects of attentional load on the network responsible for the bottom-up processing of biological motion. For this, we took a DCM approach so that we could model the hypothesis in the literature about the loci of attention, compare these hypotheses, and quantitatively examine the effects of conditions in the experimental paradigm on different connections in this network. By doing so, we can (i) obtain a better understanding of the dynamic effects of attentional load on the biological motion-related network, (ii) compare the modulations of BM and scrambled motion (SCR) on this network, and (iii) assess the differences between high-load and low-load modulation effects on this network.

Based on the previous work [1, 22, 96, 99], we hypothesize that,

1) The model that represents the attentional load theory would explain the modulations of attentional load conditions on the network.

2) Biological motion and scrambled motion would modulate the bottom-up connections with different strengths. Specifically, we expect BM stimuli to modulate significantly more positively than the SCR motion.

# Chapter 2

# Materials and Methods

The fMRI data used in this thesis is the data collected and analyzed in the study of Nizamoglu and Urgen [1].

## 2.1 Participants

The study included 31 healthy participants (23 females, 8 males) with normal or corrected-to-normal vision. The participants had no long-term use of medication for a neurological or psychiatric disorder. The participants provided their written consent and received 50 TL as compensation for their participation. The Human Research Ethics Committee of Bilkent University approved the study.

The data from the participants that showed activation in all ROIs identified in this study were used in the DCM analysis. Therefore, the data of 28 participants were used in the final DCM analysis. The details of the ROI selection are explained in Section 2.4.3.

## 2.2 Stimuli and Experimental Design

The stimuli consisted of rapid serial visual presentations (RSVP) of t-shapes in the fovea and peripheral distractors that were present in a portion of the trials. The t-shapes shown at the center of the visual field consisted of three different colors (red, green, and yellow) and two different orientations (upright and upside-down). A pseudo-random series of twelve t-shapes was shown in each trial. Each t-shape was shown for 500 ms with an interstimulus interval uniformly sampled between 250 ms and 350 ms.

There were two different tasks in the experiment that required button-press responses to specific t-shapes. The low attentional load task is to respond to red t-shapes regardless of their orientations, while the high attentional load task is to respond to upright yellow and upside-down green t-shapes. The latter requires the subjects to detect a conjunction of features, namely color and orientation. Hence, it is a more demanding task regarding attentional resources than the low-load task. This task change enables the manipulation of attentional load in the visual center without changing the visual stimulus.

The number of target t-shapes was kept constant across conditions and blocks. The tasks were assigned in blocks, with six trials in each block. The High Load (HL) and Low Load (LL) blocks are presented as a pair, and a rest block follows each pair. A single run consisted of 3 pairs of task blocks and four rest blocks. In total, there were eight runs in the experiment. In the resting blocks, there was only a cross on which participants were asked to fixate for 11 seconds on average.

In one-third of the trials, a peripheral distractor was presented simultaneously, either left or right of the central stimuli. In either case, the peripheral distractors were presented 4 degrees away from the central fixation. These distractors were either PLDs of BM or SCR. PLD of biological motion is a motion capture data of a walking person in the direction perpendicular to the plane of the screen (facing direction). The PLD of the walker consists of 13 dots and 61 frames. Scrambled motion is obtained by shuffling the initial points of the dots of the biological

motion stimulus without changing the trajectories of the dots. As a result, its overall motion does not resemble a biological motion. Each task block consisted of randomized occurrences in six trials: (i) BM distractor shown on the left, (ii) BM distractor shown on the right, (iii) SCR distractor shown on the left, (iv) SCR distractor shown on the right, and two trials of no distractor (None) conditions. The flow of a trial, task types that enable attentional load manipulation, and the block design of the experiment are summarized in Figure 2.1 [1]. Please refer to [1] for additional details on the stimuli.

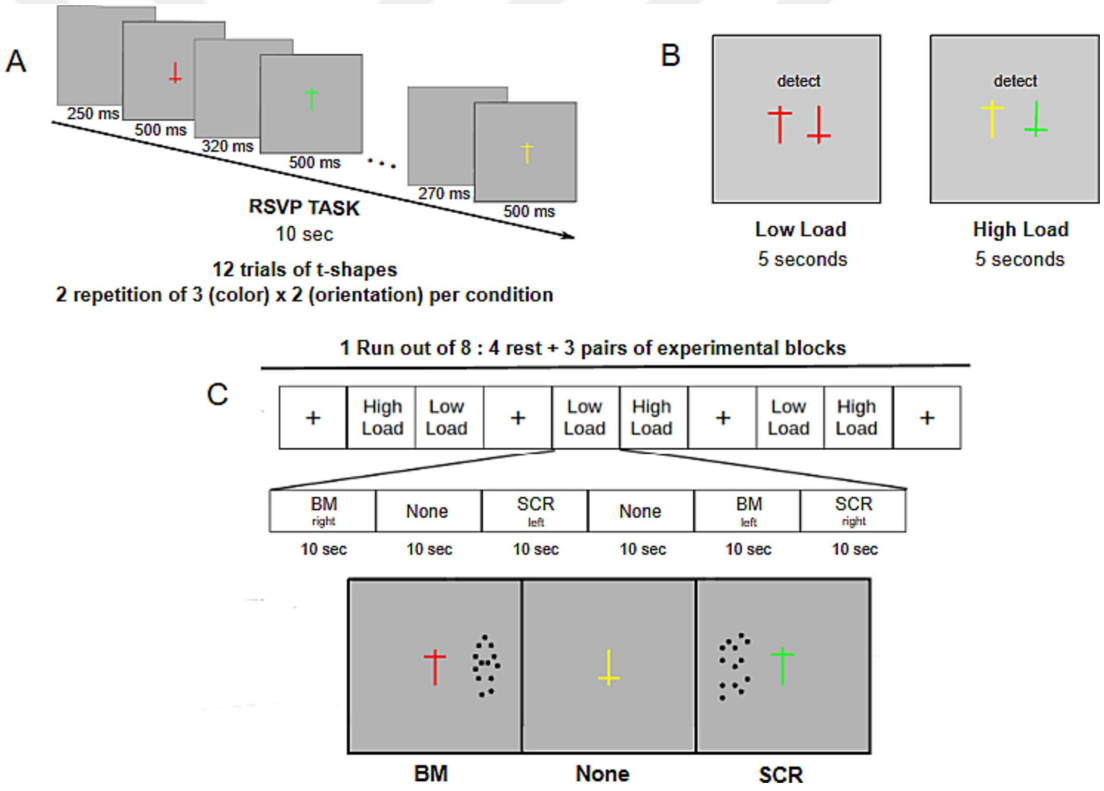



Figure 2.1: The stimuli and experiment design. (A) The flow of a single trial. For the visualization, the condition without any peripheral distractors is shown. (B) The directions are shown to the subjects for two tasks at the beginning of each block. (C) The block design of the overall experiment with the peripheral distractor conditions at the bottom. In each load block (either HL or LL), all distractor conditions (BM, None, SCR) are shown twice. Reproduced from [1] with permission.

Prior to the MRI session, participants were familiarized with the BM and SCR stimuli and performed the main task without distractors. Participants were taken to the scanning session after performing above 80% in this practice task.

## 2.3 Data Collection

The data was collected using a 3T Siemens TimTrio MR scanner with a 32-channel phase array head coil at Bilkent University National Resonance Research Center (UMRAM). An MR-compatible 32-inch LCD screen of 800x600 pixels with a 60 Hz refresh rate was used for stimuli representation. The mirror system on the head coil was located 168 cm away from the screen.

The experiment started with scanning T1-weighted high resolution structural images of participants (TR=2600 ms, TE=2.92 ms, flip angle=12°, FoV read=256 mm, FoV phase=87.5%, 176 slices with $1 \times 1 \times 1$ mm$^3$ resolution). The 227 functional images of each eight runs were obtained by utilizing gradient-echo planar imaging (TR=2000 ms, TE=22 ms, flip angle=90°, $64 \times 64$ matrix, FoV read=192 mm, 43 slices with a thickness of 2.5 mm, $3 \times 3 \times 2.5$ mm$^3$ resolution).

## 2.4 First-Level Analysis and ROI Selection

### 2.4.1 Preprocessing

The fMRI data is anatomically and functionally preprocessed using the fMRIPrep 20.1.1 [RRID:SCR_016216] [100] based on Nipype 1.5.0 [RRID:SCR_002502] [101]. The details of these preprocessing steps can be found in [1].

### 2.4.2 First-level Analysis

The conditions included in the general linear model (GLM) for the first-level analysis are decided based on the conditions included in the DCM and the contrasts used for the time-series extraction. The conditions included in the design

matrix of the GLM are HL, LL, BM, SCR, fixation block, and six motion regressors. Each regressor is convolved with the canonical hemodynamic response function of SPM12 [102]. Unless otherwise mentioned, all of the analysis steps mentioned in the following sections, including this one, are performed on the SPM12 version 7771 [102] run on MATLAB version 9.11.0 (R2021b) [103].

### 2.4.3 ROI Selection

The number of ROIs is motivated by the research questions and the experimental design. First, the requirements for investigating the research questions are determined as follows: (i) to model the effects of attention, an attention-related, hierarchically higher region is needed, (ii) to observe the effects of attentional load on the biological motion-related areas, a motion-sensitive region should be included, and (iii) to model the input region for low-level processing of the visual stimuli used in the experiment, a primary visual area is required in the model.

The ROI selection process is informed by these requirements and the results of the analyses conducted by Nizamoglu and Urgen [1]. According to the univariate analysis results in that study, a main effect of the attentional load is observed in the frontoparietal attention network in the High>Low contrast with a significant activation. Based on the reported coordinates and f-values, the left inferior parietal lobule (BA39) ($F=104.65$, $p<.05$, FWE-corrected) is selected as the attention-related region in the model. Furthermore, the multivariate pattern analysis (MVPA) results in [1] showed that the decoding accuracy is specifically higher for the early visual areas (left calcarine and right lingual gyri) and a motion-sensitive region MT, for the Low-load BM versus Low-load no distractor classification. It is important to mention that this significant accuracy for the classification in the MT area and lingual gyrus vanished for the High-load BM versus High-load no distractor discrimination. Therefore, as the motion-sensitive region in the model, this MT area where the classification accuracy for BM versus no-distractor under low-load conditions is significantly high ($T=10.5$, $p<.05$, FWE-corrected) is selected. Additionally, as the low-level input region in the

model, the left calcarine gyrus where the classification accuracy for BM versus no-distractor under low-load conditions is significantly high (T=15.51, p<.05, FWE-corrected) is selected. The ROIs' properties are summarized in Table 2.1 with their names, coordinates, and statistical results in the group-level analyses reported in [1].

Table 2.1: Summary of properties of selected ROIs. Coordinates and analyses are based on the analysis results in [1]. All statistical results are FWE-corrected for the threshold of p<.05.

| Name of the Region in the Model | Region | Coordinates | Group-level Analysis and Results |
|---|---|---|---|
| Parietal | L Inferior Parietal Lobule (BA39) | -25 -70 42 | Univariate Analysis for the Main Effect of Attentional Load High>Low contrast (F=104.65) |
| MT | L Middle Occipital Gyrus (BA19) | -49 -79 2 | Searchlight-based MVPA for Low-BM vs Low-None (T=10.5) |
| V1 | L Calcarine Gyrus (BA18) | -13 -97 -4 | Searchlight-based MVPA for Low-BM vs Low-None (T=15.51) |

The masks for the identified ROIs are created by using the MarsBaR toolbox (version 0.45) [104]. They are defined as spheres with an 8 mm radius centered around the reported coordinates in Table 2.1. Figure 2.2 shows the ROIs on the MNI-152 template [105, 106].

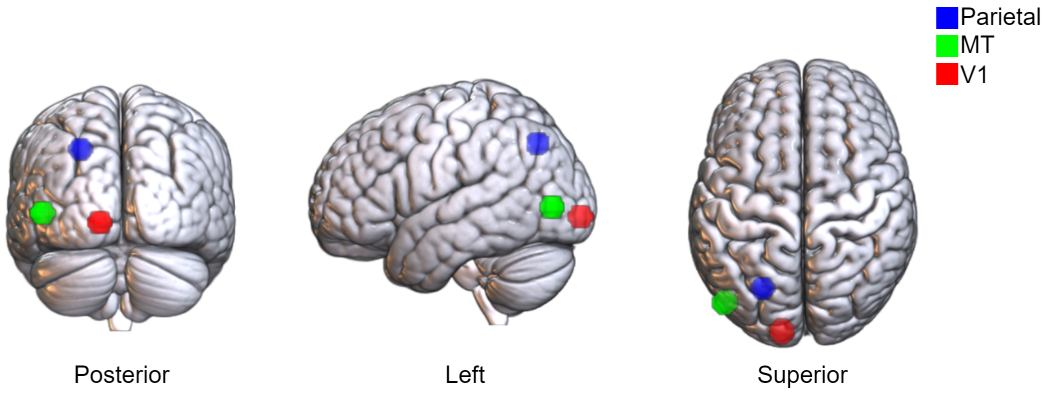



Figure 2.2: Various views of ROIs overlayed on the MNI-152 template.

## 2.5 Dynamic Causal Modeling

DCM is an effective connectivity method used to understand the coupling between regions of the brain and how the coupling strengths are affected by the experimental conditions [96]. It consists of a graph model where each node is a region of interest from the brain, and the edges between the nodes are the directed connections between these regions. These connections can be anatomically informed, or they can be hypothesis-driven and can be a part of the research question.

Each node's neural state is governed by a first-order differential equation that depends on three sets of parameters: (i) connectivity of the node with the other nodes (intrinsic connections), (ii) the modulations on these intrinsic connectivities by the experimental conditions, and (iii) the exogenous input to the system. These parameters are estimated using an expectation-maximization algorithm so that the dynamics of the neural states estimate the fMRI time series. Once the different models that model different hypotheses are estimated, they can be compared with Bayesian Model Selection (BMS) to infer the model that explains the data based on model evidence.

### 2.5.1 Timeseries Extraction

The time-series data is extracted with different contrasts for different ROIs. The time series for the Parietal region is extracted by using the t-contrast of High Load > Low Load, where the regressor for the HL condition is set as 1, the LL condition is set as -1, and the rest of the regressors are set as 0. For the MT and V1 regions, the average effect of conditions is used as the f-contrast where the weight of the regressors for all experimental conditions (HL, LL, BM, and SCR) are set as 1, and the weight of the rest of the regressors are set as 0. In both contrasts, the p-threshold is selected as $<0.05$, uncorrected, and the cluster extent threshold is set as 5 voxels.

Not all subjects had significant activations with the set thresholds in all three ROIs. The subjects without activations in any given ROIs were eliminated as the time-series extraction is not possible without suprathreshold voxels in the defined regions. Furthermore, subjects with fewer than 8 runs are removed from the analysis set as it is important for the model selection process that all subjects have an equal number of runs. As a result of these eliminations, out of the 31 participants collected in the [1], 28 of them were used in this study. The time series data is extracted using the principal eigenvariate from a sphere of radius of 8 mm centered at the local peak of the activation in a region constrained by the ROI mask obtained from MarsBaR for each of the three ROIs. This process is repeated for each of the eight runs of each subject.

### 2.5.2 Model Specification

In the bilinear DCM model specification, all models are defined using bidirectional intrinsic connections between the three ROIs. This two-way connection assumption is anatomically informed [107–110]. The inputs to the models are all defined as BM and SCR conditions, as these are conditions that drive the biological-motion-related effects in this network. All inputs are defined to be entering from the V1 for all models. Finally, the BM and SCR conditions are assumed to modulate the bottom-up connections in a hierarchical order (from V1 to MT and from MT to Parietal). This assumption is based on studies that show the hierarchical processing of biological motion information [45, 111–114].

To model the hypotheses of attentional effects, the attentional load conditions, namely HL and LL, are defined as modulators on different intrinsic connections in this network. Three DCM models that represent the hypotheses of attentional effects are as follows:

1. **Early selection hypothesis:** This hypothesis suggests that attention causes the elimination of features in the early processing steps where the

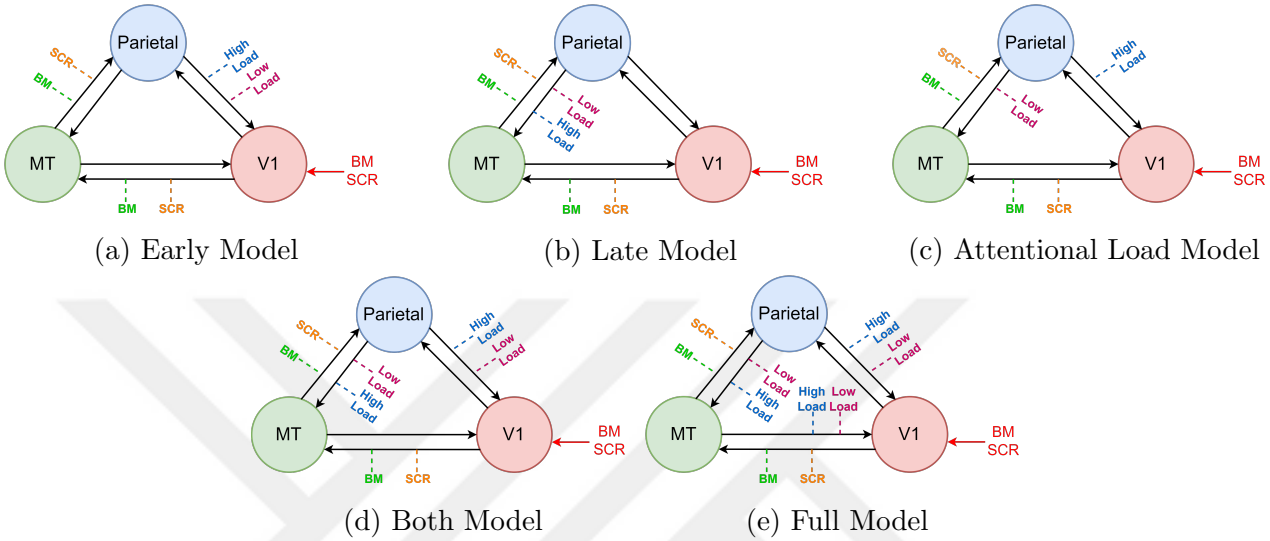
low-level features are processed. Therefore, it would be predicted that, regardless of the attentional load condition, the peripheral distractors will be eliminated early on at the V1 level since the attention is focused on the central task. Hence, the model representing the early selection hypothesis has both HL and LL as modulators on the top-down connection from Parietal to V1.

2. **Late selection hypothesis:** It states that the task-related feature filtration occurs at a later time and a higher-level region in the processing hierarchy. Thus, it predicts that the modulatory effects of load conditions should be acting at a later processing stage, regardless of the load requirement of the task. For this reason, the model for late selection has both attentional load conditions as modulators on the top-down connection from Parietal to MT.

3. **Attentional load theory:** As this theory posits that the level of elimination depends on the load of the main task, it suggests that high attentional load conditions result in elimination in the early stages due to a lack of attentional resources. In contrast, low attentional load conditions cause an elimination later in the processing. Following this, the model for the attentional load theory is defined to have the HL condition as a modulator on the top-down connection from Parietal to V1 and the LL condition as a modulator on the top-down connection from Parietal to MT.

Aside from these hypothesis-driven models, we defined two more models to have a complete model space. These two models do not depend on a hypothesis but are complementary to the proposed models. The first complementary model, which will be referred to as the Both model, has both attentional load conditions as modulators on both of the top-down connections from the Parietal (to MT and to V1). The second complementary model, the Full model, has both attentional load conditions as modulators on all of the top-down connections (from Parietal to MT, from Parietal to V1, and from MT to V1). Figure 2.3 shows the models with their modulatory connections. Separate instances of these five models are defined for each run of each subject. As a result, each subject had 40 models (5

models × 8 runs).




(a) Early Model (b) Late Model (c) Attentional Load Model

(d) Both Model (e) Full Model

Figure 2.3: The model space for the DCM analysis.

### 2.5.3 Bayesian Model Selection and Bayesian Model Averaging

After each model is defined with their respective time-series data, the parameters of the models are estimated by using the expectation-maximization algorithm. This is also called the model inversion [96]. As a result, the distributions for the parameters are obtained for the intrinsic connections, modulatory effects of experimental conditions (HL, LL, BM & SCR), and the exogenous input strengths. These models are input to the random-effects BMS to determine the model that explains the data best. As this is a random effects analysis, it assumes that the underlying model can be different for each subject. BMS utilizes the pairwise Bayesian Factor comparisons to determine the "winning model" in the given model space. For this reason, it provides a relative result rather than an absolute result. In other words, the best model determined by BMS depends on the model space.

Once the winning model is found, the Bayesian Model Averaging (BMA) method is used to average the winning model over the runs and subjects. BMA is

a random-effects method that combines the distributions obtained for parameters. It enables the combination of the Gaussian distributed parameters by accounting for the model's posterior probability that each parameter belongs to.

### 2.5.4 Statistical Tests on Model Parameters

To infer whether there is a significant difference between the modulation strengths of our experimental conditions, we conducted some statistical tests. First, we compared the difference between HL and LL conditions and BM and SCR conditions for each connection. For this, we used the non-parametric version of the independent samples t-test, the Mann-Whitney test, as the distribution of our parameters did not satisfy the normality assumptions. We then compared the strength of each connection for each condition. For instance, for the HL condition, we compared its modulation strength in all the connections that it modulated. We tested these through non-parametric ANOVA and post-hoc tests. Again, as our parameters' distributions did not satisfy the normality assumptions, we used the non-parametric versions of the tests.

# Chapter 3

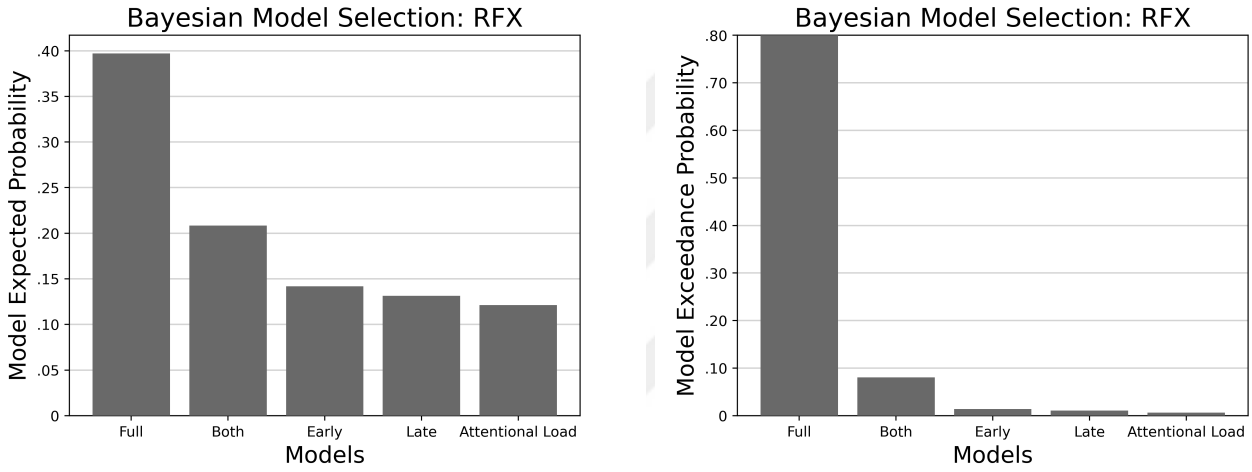
# Results

## 3.1 Bayesian Model Selection

The results of the BMS showed that the model that explained the data the best, the "winning model," is the Full model. The exceedance and expected probabilities of all the models that are obtained as a result of the BMS are shown in Figure 3.1.

As the estimated parameters are assumed to have a Gaussian distribution, as the result of the inversion operation, the mean and the variance of their distributions are obtained for each subject's model. To estimate the winning model parameters, the parameters of the winning model for each subject and each run should be combined. To achieve this, we employed the RFX BMA method. BMA enables the combination of the Gaussian distributed parameters by accounting for the model's posterior probability that each parameter belongs to. These average values of the winning model's intrinsic parameters are shown in Table 3.1, and its modulatory and exogenous parameters are shown in Figure 3.2. Here, the coupling parameters are in the units of Hz, while the self-connections of ROIs are the log scaling parameters. To determine whether the parameter values are significantly different from zero, their estimated posterior distributions' mean and

variance values are used [115]. From these MAP estimates, one can derive the probability $p(\theta > 0 \mid y)$ for each connection. These values are provided as percent values in the parenthesis next to each estimated parameter in Table 3.1, and that of the modulatory parameters are shown in Figure 3.2, next to each respective connection.




(a) Model expected probabilities.

(b) Model exceedance probabilities.

Figure 3.1: Random effects Bayesian model selection results.

Table 3.1: The parameters of intrinsic connections of the winning model. In the parentheses, the probability of the parameter being different from zero is provided as a percentage.

| | | From | | |
|---|---|---|---|---|
| | | V1 | MT | Parietal |
| To | V1 | -1.1109 (100.00) | -0.0621 (100.00) | -0.0140 (99.87) |
| | MT | 0.0214 (100.00) | -1.0378 (100.00) | 0.0783 (100.00) |
| | Parietal | -0.0026 (99.82) | 0.0074 (99.99) | -1.0460 (100.00) |

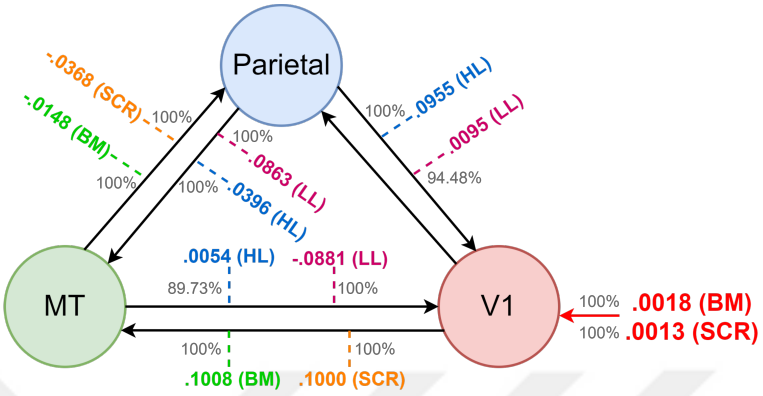


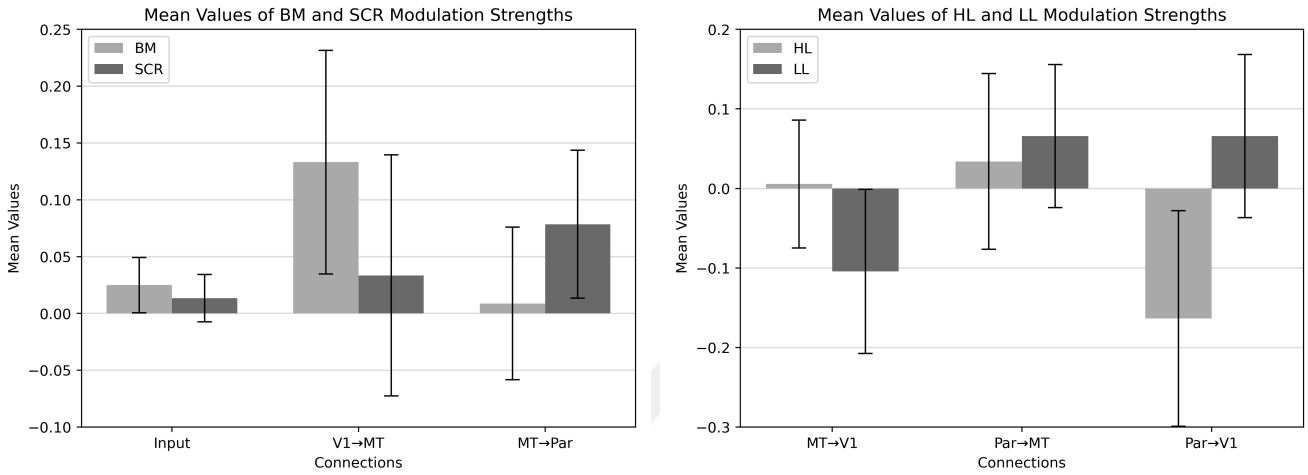

Figure 3.2: Modulatory connection strengths shown on the winning model that is the Full Model. Next to each connection, the probability of the parameter being different from zero is provided as a percentage.

## 3.2 Statistical Tests on Model Parameters

The results of the pairwise comparisons between the modulatory conditions on the same connections are provided in Table 3.2, and the mean values of parameter values are shown in Figure 3.3. The non-parametric t-test, the Mann-Whitney $U$ test, did not yield any significant results for any of the connections.

Table 3.2: Results of Mann-Whitney $U$ test on the modulation strengths on the same connections. p-values are uncorrected.

| Conditions | Connections | $U$ | p |
|---|---|---|---|
| HL vs LL | MT→V1 | 26802 | 0.211 |
| | Par→MT | 24108 | 0.475 |
| | Par→V1 | 22894 | 0.109 |
| BM vs SCR | Input | 25345 | 0.852 |
| | V1→MT | 27712 | 0.056 |
| | MT→Par | 25049 | 0.978 |




(a) BM and SCR.

(b) HL and LL.

Figure 3.3: Mean values of the modulatory parameters on the same connections. The error bars show the 95% confidence interval.

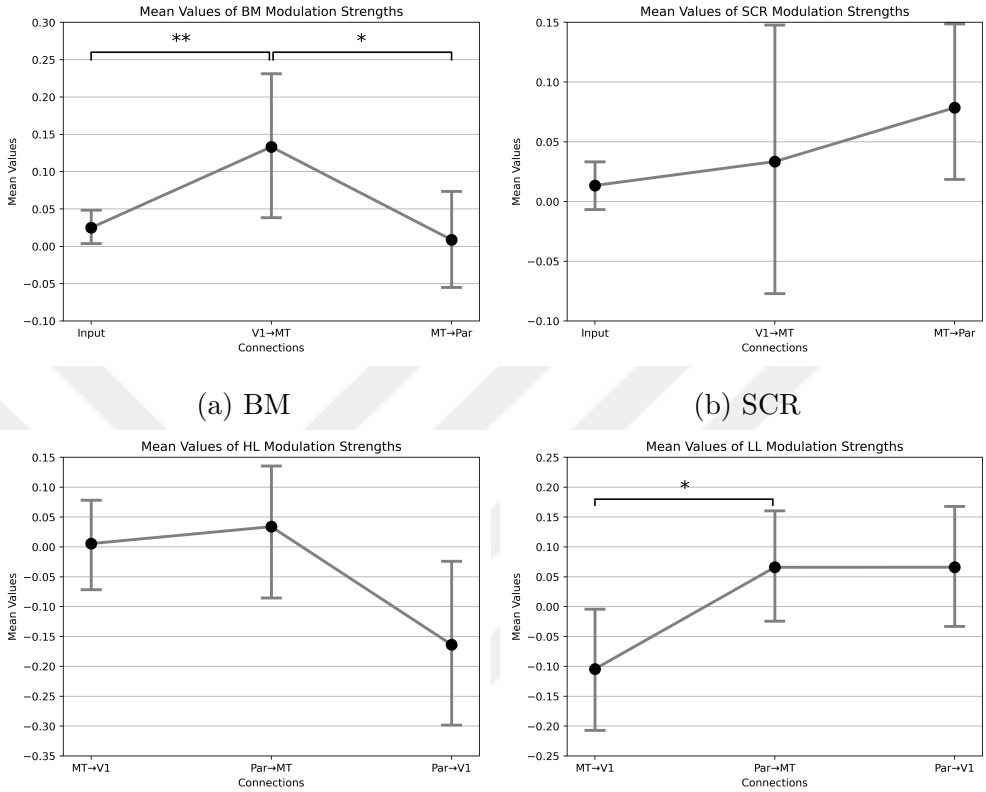
Another way to compare the parameters is to compare the strengths of modulations for a condition on different connections. For instance, comparing the strengths of modulations by the BM condition on all the connections that it modulated: input, V1 to MT, and MT to Parietal. As there are three connections for each of the conditions and since the distributions of parameters violate the normality conditions, the non-parametric version of one-way ANOVA, the Kruskar-Wallis test, is applied for this comparison. Then, for the post-hoc tests, Dunn's test is applied to the connection pairs since it is a non-parametric alternative to the independent samples t-test. The result of these tests can be seen in Table 3.3, and the mean values of the modulation strengths of each condition on each connection are shown in Figure 3.4. As shown in Table 3.3, the Kruskar-Wallis test yielded no significant results for HL and SCR conditions, while it yielded significant results for BM and LL conditions. Following this, Dunn's test was applied, and the results showed that, for BM, the modulation on the connection from V1 to MT was significantly stronger than the modulation on the connection from MT to Parietal. For the LL, the modulation on the connection from MT to V1 was significantly stronger than the modulation on the connection from Parietal to MT. The results of Dunn's test are summarized in Table 3.4.

Table 3.3: Results of Kruskar-Wallis test on modulation strengths of each condition.

| Conditions | Factor | $H$ | df | p |
|---|---|---|---|---|
| BM | Connections | 10.000 | 2 | 0.007 |
| SCR | Connections | 0.617 | 2 | 0.735 |
| HL | Connections | 2.416 | 2 | 0.299 |
| LL | Connections | 7.442 | 2 | 0.024 |

Table 3.4: Results of Dunn's test on the pairwise modulation strengths of the connections of BM and LL conditions. p-values are Bonferroni corrected.

| Conditions | Comparison | | | z | p |
|---|---|---|---|---|---|
| | Input | - | MT→Par | -0.522 | 1.000 |
| BM | Input | - | V1→MT | -2.962 | 0.009 |
| | MT→Par | - | V1→MT | -2.440 | 0.044 |
| | MT→V1 | - | Par→MT | -2.624 | 0.026 |
| LL | MT→V1 | - | Par→V1 | -1.957 | 0.151 |
| | Par→MT | - | Par→V1 | 0.667 | 1.000 |




(a) BM (b) SCR

(c) HL (d) LL

Figure 3.4: Mean values of the modulatory parameters for each condition. The error bars show the 95% confidence interval (*: $p < .05$, **:$p < .01$, Bonferroni corrected).

# Chapter 4

# Discussion

Biological motion carries evolutionarily significant information to sustain safety and facilitate social interactions. Therefore, understanding the neural basis of its perception is crucial. The literature has mostly identified the regions that play a part in biological motion perception. However, the dynamics and the effective connectivities between these regions also hold an important place in understanding the mechanisms through which this perception is achieved. Notably, how attentional load affects it is a matter of great concern since, in our daily lives, we are exposed to not sole biological motion, but we perceive biological motion most of the time in our peripheral vision while on a task. To this end, we adopted a DCM approach for fMRI data where the bottom-up biological motion perception is investigated using different attentional load conditions. To the best of our knowledge, this study is the first study that utilized DCM within an attentional load paradigm for biological motion perception.

Based on the previous works and the questions existing in the literature, we constructed a model space consisting of three models that stemmed from theories on the locus of attention in the literature and two complementary models. We hypothesized that the model representing the perceptual load theory would prevail, and we expected the bottom-up modulations of BM and SCR motion conditions to have different strengths, as BM is a more meaningful stimulus. We found the

winning model to be a model we call the Full Model, where all the top-down connections in our network are modulated by both high and low load conditions. We also found no statistically significant difference between BM and SCR modulations, as well as HL and LL modulations in the winning model parameters. Yet, we observed that there are significant differences between the modulations of BM on different connections. A similar observation is also valid for LL modulations. The implications of these findings will be discussed in this chapter.

## 4.1 Full Model as the Winning Model

Differing from our hypothesis, the model that explained the data the best turned out to be the Full Model. This result provides evidence for the view that attention is a distributed top-down effect that alters the processes on many levels of bottom-up perception [116]. This is a sensible suggestion as top-down selective attention (motivated by the goals) is known to increase the firing rates of neurons that encode the attended stimulus [117]. Since such feature processing exists not only at a single level but also through a hierarchical line of processes, it is plausible that attentional mechanisms modulate the processing at these different stages simultaneously. At this point, examining the differences between high and low load conditions for each connection and the differences between modulations on connections for each condition can provide a more comprehensive explanation for the dynamics. As there are two sets of modulatory conditions in our models, the bottom-up due to BM and SCR and the top-down due to HL and LL, the results related to these will be discussed separately in the following sections.

The reason for the prevalence of the Full Model may seem to be the number of modulatory connections in this model. Since the Full Model has the most modulatory connections, one can attribute its better performance in explaining the data to this. However, the model selection method, BMS, considers the model evidence estimated by the free energy, which accounts for the complexity of the model. Hence, we believe such an explanation for this finding is unlikely.

All of the intrinsic connection parameters of the winning model are significantly different from zero, in line with the known anatomical connections between these regions [107–110]. Magnitude-wise, the strongest connection is observed from the Parietal to MT region, which is positive, followed by the MT to V1 connection, which is negative (self-connections excluded). This is in part consistent with the earlier research where stronger effective connectivity from the Parietal to MT region is reported when compared to the MT to Parietal connectivity [118, 119], but the negative connectivity from V5 to V1 differs from the findings of Stephan et al. [119] as they reported positive yet relatively strong intrinsic connectivity parameter from the MT and V1. This discrepancy can be accounted for by the fact that in Stephan and colleagues' experimental conditions, the motion is perceived in a top-down fashion, while in our experimental conditions, the BM is perceived in a bottom-up manner and even instructed to be ignored.

### 4.1.1 Top-down Modulations of High Load and Low Load Conditions

The winning model revealed that all of the top-down connections are modulated by both of the attentional load conditions. This suggests that rather than a focused filter, attentional modulations affect the processing at multiple levels in the BM perception pipeline. When the HL and LL modulations were compared on each connection they modulated using a non-parametric t-test, no significant difference was found between their strengths. The lack of significant difference between the modulations of load connections cannot be attributed to the lack of difference between loads of the tasks given in the experimental conditions. It is out of concern as Nizamoglu and Urgen reported significant differences in behavioral results between two load conditions and fMRI results supporting the increased load in high load conditions with increased Parietal activations and decreased load with increased DMN activations [1].

The test between the modulation strengths in connections by each condition

revealed that the LL condition has significantly higher modulation on the connection from the Parietal to MT when compared to its modulation on the connection from MT to V1, see Figure 3.4. No significant differences are found between the modulations of HL on different connections. The difference between MT→V1 and Parietal→MT in the LL modulations can be explained by the spillover of attentional resources on the BM stimuli, which results in sensory competition between the main task and the peripheral distractor as they have concurrently presented. The absence of such negative modulations by HL on the same connection is also consistent with this view of competition [120].

Compared to the statistical findings, among the modulatory parameters, the LL modulation on the connection from the Parietal to the V1 and the HL modulation on the connection from MT to V1 were found not to be significantly different than zero ($p > .05$), see Figure 3.2. When the strengths of modulations of the winning model are considered, the higher modulation of HL condition on the Parietal→V1 compared to the LL modulation, which is not significantly different than zero, is evident. Also, on the Parietal→MT connection, the strength of LL is greater than HL, even though this difference was not found to be significant. A final important point concerns the modulations on the MT→V1 connection where there is a negative LL modulation while HL modulation is not significantly different than zero. When these are considered, we may argue that the winning model parameters, reported in Figure 3.2, partially support the predictions of the attentional load theory where the HL condition caused a higher modulation on the early level area V1 than the LL, and LL caused a higher modulation on the later level processing area MT than the HL condition. Yet, attentional load theory does not predict the modulation of conditions from MT to V1, where our model found the LL condition is negatively modulating. As explained above for the statistical tests, this negative modulation may be attributed to the competition between the peripheral and central stimuli.

The difference between the means shown in Figure 3.3 and Figure 3.2 is due to the fact that the BMA result takes the model evidence into account and computes the average of the parameters weighted by this evidence while the simple average is computed over all runs and all subjects for the statistical tests. Therefore,

this difference shows us that in a Bayesian framework, such as DCM, where the parameter posteriors are Gaussians, using frequentist tests by only considering the mean values of the posteriors may yield different results that may not necessarily be consistent, albeit widely used in the literature with DCM approach [115].

When the literature is considered, the DCM study with attentional load conditions by Desseilles and colleagues reported that the winning model included modulations only by high load condition but not by low load condition in the healthy subjects [99]. On the other hand, the modulation by the low load condition was present in the depression patient group. In this aspect, our results are inconsistent with their findings, where our winning model had both HL and LL modulations, and all of our subjects were healthy subjects. However, a difference between their study and ours can also be responsible for this inconsistency: Their DCM models were nonlinear, where the load conditions were provided as input to the Parietal node, and this node, in turn, modulated the connectivity between V1 and V4 while our DCM models were bilinear where the load conditions directly modulated the top-down connections.

### 4.1.2 Bottom-up Modulations of Biological Motion and Scrambled Motion

In our models, we assumed that both BM and SCR are processed in a bottom-up and hierarchical manner, following a path of V1→MT→Parietal regions. Contrary to our hypotheses, we found no significant difference between the modulation strengths of these two conditions as a result of the Mann-Whitney $U$ test. Although unexpected based on the previous literature [11, 13, 53, 121], this result can be explained by the findings of Nizamoglu and Urgen's study, where the data originates from [1]. In their study, they also did not find a significant difference between the BM and SCR stimuli. As a possible explanation, they suggest the subjects' possible inability to recognize the BM stimuli. This view is also supported by the lack of STS activation for BM and SCR stimulus in their study. As the same data is used in this study, the same explanation is valid.

When the modulations of BM and SCR are inspected separately on each connection they modulated, significant differences are observed in two connection pairs for BM, while no significant differences are observed for SCR. For the BM modulations, significant differences are observed for (i) input strength and the modulation on the connection from V1 to MT and (ii) the difference between the modulations on connections from MT to Parietal and from V1 to MT, see Table 3.4. This finding that BM modulates the flow of information from V1 to MT more than the other connections, namely the input to V1 and from MT to Parietal, can be explained by the hierarchical processing of BM [22, 45, 47]. As an input to the V1, BM may not constitute a high portion of the visual information since the fixation is on the center. Yet, it is likely that it constitutes a very high proportion of the information flow from V1 to MT as this pathway is more responsive to motion stimuli and, hence, likely to be activated/modulated by such motion stimuli. On the other hand, the modulation of the connection from MT to the Parietal is also significantly less than the modulation of the connection of V1 to MT. This decrease in the modulation of connectivity from MT to the Parietal region can be attributed to the bottom-up perception of BM. While for the top-down perception of BM, the parietal region is reported as an encoder of intentions, the activation for parietal regions was not widely reported for the bottom-up perception of BM, even said to be activated with directed attention [24, 53, 122]. Therefore, this finding is in agreement with the previous literature.

In addition, the fact that BM has significant differences in its modulations on different connections, while SCR does not, may still hint at a difference in the processing of these two types of stimuli. Specifically, this may be accepted as evidence for the idea that the relative modulation of connections can have an effect on the recognition and discrimination of different motion stimuli. This idea can be a problem for future studies that investigate the difference between the processing of BM and SCR.

## 4.2 Limitations

As mentioned before, using frequentist tests with the Bayesian framework of DCM may be disadvantageous as these approaches will not consider the estimated variances of the posterior probabilities. One way to solve this problem can be to use the Parametric Empirical Bayes (PEB) approach, which establishes a hierarchical Bayesian model [123]. Thus, replicating this study with a PEB approach would also contribute to the validation of our findings.

Even though PLDs provide abstracted biological motion stimuli without introducing confounders such as colors, patterns, or unrelated background motion, they are known to produce fewer activations when compared with more naturalistic stimuli such as video actions [124]. Hence, using more ecologically valid naturalistic videos or live actions instead of PLDs may result in both stronger effects and a more widespread area of activation, possibly stimulating STS and Parietal regions as well. Additionally, BM perception is not necessarily a lateralized process [32, 53, 125]. However, due to the limitations of activated areas, the ROIs used in this study were confined to the left hemisphere. Using video peripheral stimuli may also resolve this shortcoming by yielding a higher activation in both hemispheres.

Furthermore, the limited regions activated due to the peripheral stimuli restricted the involvement of more biological motion-specific areas such as STS in this study. Therefore, it should be noted that the activations and modeled effects are not specific to BM, as the difference between the SCR and BM has not been investigated.

## 4.3 Future Directions

While our study showed the dynamics of attentional load effects on the bottom-up perception of BM, the exact mechanisms of these effects are yet to be explored.

Mechanistic computational models for the attentional load effects on the bottom-up perception are required. These models can be informed by our results, which show that the attentional load effects take place in several stages through the bottom-up processing.

An improvement to this study can be achieved by using ecologically valid videos and obtaining bottom-up processing activations in more areas throughout the BM perception pipeline, such as STS, parietal, and premotor regions. By doing so, future studies may increase the number of nodes in the BM processing from V1 and MT to several regions and try to understand where and how much these attentional load effects take part in this network. Such a study would also improve our understanding of the interaction between action observation and attentional networks.

# Chapter 5

# Conclusion

In conclusion, this study examined the connectivity of the cortical regions in biological motion perception, namely, V1, MT, and Parietal, during different attentional load conditions. These regions are determined as a result of the findings of Nizamoglu and Urgen, respectively, which showed that (i) occipitotemporal region activation was persistent in both load conditions, (ii) the peripheral BM stimuli conditions could be decoded from the motion-sensitive area MT in the low load condition but not in the high load condition and (iii) an increased fronto-parietal region activation for the high load condition relative to low load condition [1]. Using the data collected in this study, we constructed dynamic causal models with bi-directional intrinsic connections between these regions, bottom-up hierarchical modulations by BM and SCR conditions, and various top-down modulations by HL and LL conditions that represent different hypotheses of selective attention in the literature. Our BMS results showed that, unlike the mainstream hypothesis on the locus of attention, the model that has modulations on all the top-down connections by both of the attentional load conditions explained the data the best. This finding suggests a distributed effect of attention on the bottom-up biological motion perception hierarchy and load-independent modulation. Also, the statistical tests on the parameters showed that there were no significant differences in the modulation strengths of HL-LL and BM-SCR pairs on the same connections. Despite that, we observed differences in the modulations of BM on

different connections as well as that of LL, but not for HL and SCR. This may still be accepted as a piece of evidence for the differential processing of BM and SCR conditions. For the attentional load conditions, this may show the spillover of perceptual resources on the BM stimuli, which in turn causes a competition that negatively modulates the MT to V1 connection in the LL condition only.

# Bibliography


[1] H. Nizamoglu and B. A. Urgen, "Neural processing of bottom-up perception of biological motion under attentional load," *Vision Research*, vol. 214, p. 108328, 2024.

[2] E. Goldstein and J. Brockmole, *Sensation and Perception*. Cengage Learning, 2016.

[3] E. B. Goldstein, *Cognitive psychology: Connecting mind, research and everyday experience*. Cengage Learning Stamford, CT, 2015.

[4] G. Johansson, "Visual perception of biological motion and a model for its analysis," *Perception & psychophysics*, vol. 14, pp. 201–211, 1973.

[5] N. F. Troje, "What Is Biological Motion? Definition, Stimuli, and Paradigms," in *Social Perception: Detection and Interpretation of Animacy, Agency, and Intention*, The MIT Press, 08 2013.

[6] F. Simion, L. Bardi, E. Mascalzoni, and L. Regolin, "From Motion Cues to Social Perception: Innate Predispositions," in *Social Perception: Detection and Interpretation of Animacy, Agency, and Intention*, The MIT Press, 08 2013.

[7] K. Alaerts, E. Nackaerts, P. Meyns, S. P. Swinnen, and N. Wenderoth, "Action and emotion recognition from point light displays: an investigation of gender differences," *PloS one*, vol. 6, no. 6, p. e20989, 2011.

[8] O. C. Oguz, B. Aydin, and B. A. Urgen, "Biological motion perception in the theoretical framework of perceptual decision-making: An event-related potential study," *Vision research*, vol. 218, p. 108380, 2024.

[9] M. Edwards, J. Deng, and X. Xie, "From pose to activity: Surveying datasets and introducing converse," *Computer Vision and Image Understanding*, vol. 144, pp. 73–105, 2016.

[10] J. Thompson, *Biological motion perception.*, pp. 427–442. Cambridge handbooks in psychology., New York, NY, US: Cambridge University Press, 2015.

[11] E. D. Grossman and R. Blake, "Brain areas active during visual perception of biological motion," *Neuron*, vol. 35, no. 6, pp. 1167–1175, 2002.

[12] A. P. Saygin, "Superior temporal and premotor brain areas necessary for biological motion perception," *Brain*, vol. 130, no. 9, pp. 2452–2461, 2007.

[13] M. V. Peelen, A. J. Wiggett, and P. E. Downing, "Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion," *Neuron*, vol. 49, no. 6, pp. 815–822, 2006.

[14] S. Caspers, K. Zilles, A. R. Laird, and S. B. Eickhoff, "ALE meta-analysis of action observation and imitation in the human brain," *Neuroimage*, vol. 50, no. 3, pp. 1148–1167, 2010.

[15] K. Nelissen, E. Borra, M. Gerbella, S. Rozzi, G. Luppino, W. Vanduffel, G. Rizzolatti, and G. A. Orban, "Action observation circuits in the macaque monkey cortex," *Journal of Neuroscience*, vol. 31, no. 10, pp. 3743–3756, 2011.

[16] N. N. Oosterhof, S. P. Tipper, and P. E. Downing, "Crossmodal and action-specific: neuroimaging the human mirror neuron system," *Trends in cognitive sciences*, vol. 17, no. 7, pp. 311–318, 2013.

[17] A. Inuggi, C. Campus, R. Vastano, G. Saunier, A. Keuroghlanian, and T. Pozzo, "Observation of point-light-walker locomotion induces motor resonance when explicitly represented; an EEG source analysis study," *Frontiers in psychology*, vol. 9, p. 309173, 2018.

[18] D. Jokisch, I. Daum, B. Suchan, and N. F. Troje, "Structural encoding and recognition of biological motion: evidence from event-related potentials and source analysis," *Behavioural brain research*, vol. 157, no. 2, pp. 195–204, 2005.

[19] A. Puce and D. Perrett, "Electrophysiology and brain imaging of biological motion," *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, vol. 358, no. 1431, pp. 435–445, 2003.

[20] G. Rizzolatti and L. Craighero, "The mirror-neuron system," *Annu. Rev. Neurosci.*, vol. 27, pp. 169–192, 2004.

[21] G. Rizzolatti and L. Fogassi, "The mirror mechanism: recent findings and perspectives," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 369, no. 1644, p. 20130420, 2014.

[22] J. Thompson and R. Parasuraman, "Attention, biological motion, and action recognition," *Neuroimage*, vol. 59, no. 1, pp. 4–13, 2012.

[23] M. Mishkin and L. G. Ungerleider, "Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys," *Behavioural brain research*, vol. 6, no. 1, pp. 57–77, 1982.

[24] J. Jastorff and G. A. Orban, "Human functional magnetic resonance imaging reveals separation and integration of shape and motion cues in biological motion processing," *Journal of Neuroscience*, vol. 29, no. 22, pp. 7315–7329, 2009.

[25] E. D. Grossman, L. Battelli, and A. Pascual-Leone, "Repetitive TMS over posterior STS disrupts perception of biological motion," *Vision research*, vol. 45, no. 22, pp. 2847–2853, 2005.

[26] B. M. van Kemenade, N. Muggleton, V. Walsh, and A. P. Saygin, "Effects of TMS over premotor and superior temporal cortices on biological motion perception," *Journal of Cognitive Neuroscience*, vol. 24, no. 4, pp. 896–904, 2012.

[27] A. P. Saygin, S. M. Wilson, D. J. Hagler, E. Bates, and M. I. Sereno, "Point-light biological motion perception activates human premotor cortex," *Journal of Neuroscience*, vol. 24, no. 27, pp. 6181–6188, 2004.

[28] M. Hirai and A. Senju, "The two-process theory of biological motion processing," *Neuroscience  Biobehavioral Reviews*, vol. 111, pp. 114–124, 2020.

[29] E. D. Grossman, N. L. Jardine, and J. A. Pyles, "fMR-adaptation reveals invariant coding of biological motion on human STS," *Frontiers in human neuroscience*, vol. 4, p. 954, 2010.

[30] J. W. Kable and A. Chatterjee, "Specificity of action representations in the lateral occipitotemporal cortex," *Journal of Cognitive Neuroscience*, vol. 18, no. 9, pp. 1498–1517, 2006.

[31] A. J. Wiggett and P. E. Downing, "Representation of action in occipitotemporal cortex," *Journal of Cognitive Neuroscience*, vol. 23, no. 7, pp. 1765–1780, 2011.

[32] L. M. Vaina, J. Solomon, S. Chowdhury, P. Sinha, and J. W. Belliveau, "Functional neuroanatomy of biological motion perception in humans," *Proceedings of the National Academy of Sciences*, vol. 98, no. 20, pp. 11656–11661, 2001.

[33] K. Saleem, W. Suzuki, K. Tanaka, and T. Hashikawa, "Connections between anterior inferotemporal cortex and superior temporal sulcus regions in the macaque monkey," *Journal of Neuroscience*, vol. 20, no. 13, pp. 5083–5101, 2000.

[34] T. Jellema and D. I. Perrett, "Neural representations of perceived bodily actions using a categorical frame of reference," *Neuropsychologia*, vol. 44, no. 9, pp. 1535–1546, 2006.

[35] A. F. de C. Hamilton and S. T. Grafton, "Action outcomes are represented in human inferior frontoparietal cortex," *Cerebral Cortex*, vol. 18, no. 5, pp. 1160–1168, 2008.

[36] A. F. d. C. Hamilton and S. T. Grafton, "Goal representation in human anterior intraparietal sulcus," *Journal of Neuroscience*, vol. 26, no. 4, pp. 1133–1137, 2006.

[37] L. Shmuelof and E. Zohary, "Dissociation between ventral and dorsal fMRI activation during object and action recognition," *Neuron*, vol. 47, no. 3, pp. 457–470, 2005.

[38] J. Jastorff, C. Begliomini, M. Fabbri-Destro, G. Rizzolatti, and G. A. Orban, "Coding observed motor acts: different organizational principles in the parietal and premotor cortex of humans," *Journal of neurophysiology*, vol. 104, no. 1, pp. 128–140, 2010.

[39] J. H. Kaas and I. Stepniewska, "Evolution of posterior parietal cortex and parietal-frontal networks for specific actions in primates," *Journal of Comparative Neurology*, vol. 524, no. 3, pp. 595–608, 2016.

[40] B. A. Urgen and G. A. Orban, "The unique role of parietal cortex in action observation: Functional organization for communicative and manipulative actions," *NeuroImage*, vol. 237, p. 118220, 2021.

[41] G. Buccino, F. Binkofski, G. R. Fink, L. Fadiga, L. Fogassi, V. Gallese, R. J. Seitz, K. Zilles, G. Rizzolatti, and H.-J. Freund, "Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study," in *Social neuroscience*, pp. 133–141, Psychology Press, 2013.

[42] K. J. Wheaton, J. C. Thompson, A. Syngeniotis, D. F. Abbott, and A. Puce, "Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex," *Neuroimage*, vol. 22, no. 1, pp. 277–288, 2004.

[43] S. H. Johnson-Frey, F. R. Maloof, R. Newman-Norlund, C. Farrer, S. Inati, and S. T. Grafton, "Actions or hand-object interactions? human inferior

frontal cortex and action observation," *Neuron*, vol. 39, no. 6, pp. 1053–1058, 2003.

[44] M. Iacoboni, I. Molnar-Szakacs, V. Gallese, G. Buccino, J. C. Mazziotta, and G. Rizzolatti, "Grasping the intentions of others with one's own mirror neuron system," *PLoS biology*, vol. 3, no. 3, p. e79, 2005.

[45] M. A. Giese and T. Poggio, "Neural mechanisms for the recognition of biological movements," *Nature Reviews Neuroscience*, vol. 4, no. 3, pp. 179–192, 2003.

[46] J. Lange and M. Lappe, "A model of biological motion perception from configural form cues," *Journal of Neuroscience*, vol. 26, no. 11, pp. 2894–2906, 2006.

[47] F. Fleischer, V. Caggiano, P. Thier, and M. A. Giese, "Physiologically inspired model for the visual recognition of transitive hand actions," *Journal of Neuroscience*, vol. 33, no. 15, pp. 6563–6580, 2013.

[48] I. M. Thornton, R. A. Rensink, and M. Shiffrar, "Active versus passive processing of biological motion," *Perception*, vol. 31, no. 7, pp. 837–853, 2002.

[49] B. A. Eriksen and C. W. Eriksen, "Effects of noise letters upon the identification of a target letter in a nonsearch task," *Perception & Psychophysics*, vol. 16, no. 1, pp. 143–149, 1974.

[50] I. M. Thornton and Q. C. Vuong, "Incidental processing of biological motion," *Current Biology*, vol. 14, no. 12, pp. 1084–1089, 2004.

[51] H. Ikeda, K. Watanabe, and P. Cavanagh, "Crowding of biological motion stimuli," *Journal of Vision*, vol. 13, no. 4, pp. 20–20, 2013.

[52] A. S. Safford, E. A. Hussey, R. Parasuraman, and J. C. Thompson, "Object-based attentional modulation of biological motion processing: spatiotemporal dynamics using functional magnetic resonance imaging and electroencephalography," *Journal of Neuroscience*, vol. 30, no. 27, pp. 9064–9073, 2010.

[53] A. P. Saygin and M. I. Sereno, "Retinotopy and attention in human occipital, temporal, parietal, and frontal cortex," *Cerebral cortex*, vol. 18, no. 9, pp. 2158–2168, 2008.

[54] E. C. Cherry, "Some experiments on the recognition of speech, with one and with two ears," *The Journal of the acoustical society of America*, vol. 25, no. 5, pp. 975–979, 1953.

[55] M. W. Eysenck, "Attention: Beyond cherry's (1953) cocktail party problem," *Cognitive psychology: Revisiting the classic studies. London: SAGE*, 2015.

[56] N. Moray, "Attention in dichotic listening: Affective cues and the influence of instructions," *Quarterly journal of experimental psychology*, vol. 11, no. 1, pp. 56–60, 1959.

[57] N. Wood and N. Cowan, "The cocktail party phenomenon revisited: how frequent are attention shifts to one's name in an irrelevant auditory channel?," *Journal of Experimental Psychology: Learning, Memory, and Cognition*, vol. 21, no. 1, p. 255, 1995.

[58] J. Gray and A. Wedderburn, "Shorter articles and notes grouping strategies with simultaneous stimuli," *Quarterly Journal of Experimental Psychology*, vol. 12, no. 3, pp. 180–184, 1960.

[59] J. L. Lewis, "Semantic processing of unattended messages using dichotic listening.," *Journal of experimental psychology*, vol. 85, no. 2, p. 225, 1970.

[60] K. Hugdahl, R. Westerhausen, K. Alho, S. Medvedev, M. Laine, and H. Hämäläinen, "Attention and cognitive control: unfolding the dichotic listening story," *Scandinavian journal of psychology*, vol. 50, no. 1, pp. 11–22, 2009.

[61] D. E. Broadbent, *Perception and communication.* Elmsford, NY, US: Pergamon Press, 1958.

[62] G. Sperling, "The information available in brief visual presentations.," *Psychological monographs: General and applied*, vol. 74, no. 11, p. 1, 1960.

[63] U. Neisser, "Selective reading: a method for the study of visual attention," in *19th International Congress of Psychology, London*, 1969.

[64] A. M. Treisman and J. G. Riley, "Is selective attention selective perception or selective response? a further test.," *Journal of Experimental Psychology*, vol. 79, no. 1p1, p. 27, 1969.

[65] J. Von Wright, "On selection in visual immediate memory," *Acta Psychologica*, vol. 33, pp. 280–292, 1970.

[66] C. R. Snyder, "Selection, inspection, and naming in visual search.," *Journal of experimental psychology*, vol. 92, no. 3, p. 428, 1972.

[67] J. Von Wright, "Selection in visual immediate memory," *Quarterly journal of experimental psychology*, vol. 20, no. 1, pp. 62–68, 1968.

[68] J. A. Deutsch and D. Deutsch, "Attention: Some theoretical considerations.," *Psychological review*, vol. 70, no. 1, p. 80, 1963.

[69] D. A. Norman, "Toward a theory of memory and attention.," *Psychological review*, vol. 75, no. 6, p. 522, 1968.

[70] S. W. Keele and W. T. Neill, "Chapter 1 - mechanisms of attention," in *Perceptual Processing* (E. C. Carterette and M. P. Friedman, eds.), pp. 3–47, Academic Press, 1978.

[71] J. Duncan, "The locus of interference in the perception of simultaneous stimuli.," *Psychological review*, vol. 87, no. 3, p. 272, 1980.

[72] J. Miller, "Priming is not necessary for selective-attention failures: Semantic effects of unattended, unprimed letters," *Perception & Psychophysics*, vol. 41, no. 5, pp. 419–434, 1987.

[73] N. Moray, "Attention in dichotic listening: Affective cues and the influence of instructions," *Quarterly journal of experimental psychology*, vol. 11, no. 1, pp. 56–60, 1959.

[74] J. R. Stroop, "Studies of interference in serial verbal reactions.," *Journal of experimental psychology*, vol. 18, no. 6, p. 643, 1935.

[75] D. Kahneman and A. Treisman, "Changing views of attention and automaticity," *Varieties of attention*, pp. 29–61, 1984.

[76] N. Lavie and Y. Tsal, "Perceptual load as a major determinant of the locus of selection in visual attention," *Perception & psychophysics*, vol. 56, pp. 183–197, 1994.

[77] D. Lamy, A. B. Leber, and H. E. Egeth, "Selective attention," *Handbook of Psychology, Second Edition*, vol. 4, 2012.

[78] N. Lavie, "Distracted and confused?: Selective attention under load," *Trends in cognitive sciences*, vol. 9, no. 2, pp. 75–82, 2005.

[79] G. Manini, F. Botta, E. Martín-Arévalo, V. Ferrari, and J. Lupiáñez, "Attentional capture from inside vs. outside the attentional focus," *Frontiers in Psychology*, vol. 12, p. 758747, 2021.

[80] G. Murphy, J. A. Groeger, and C. M. Greene, "Twenty years of load theory—where are we now, and where should we go next?," *Psychonomic bulletin & review*, vol. 23, pp. 1316–1340, 2016.

[81] G. Rees, C. D. Frith, and N. Lavie, "Modulating irrelevant motion perception by varying attentional load in an unrelated task," *Science*, vol. 278, no. 5343, pp. 1616–1619, 1997.

[82] S. Schwartz, P. Vuilleumier, C. Hutton, A. Maravita, R. J. Dolan, and J. Driver, "Attentional load and sensory competition in human vision: modulation of fMRI responses by load at fixation during task-irrelevant stimulation in the peripheral visual field," *Cerebral cortex*, vol. 15, no. 6, pp. 770–786, 2005.

[83] H. Benoni and Y. Tsal, "Conceptual and methodological concerns in the theory of perceptual load," *Frontiers in Psychology*, vol. 4, 2013.

[84] Y. Tsal and H. Benoni, "Diluting the burden of load: perceptual load effects are simply dilution effects.," *Journal of Experimental Psychology: Human Perception and Performance*, vol. 36, no. 6, p. 1645, 2010.

[85] M. Corbetta and G. L. Shulman, "Control of goal-directed and stimulus-driven attention in the brain," *Nature reviews neuroscience*, vol. 3, no. 3, pp. 201–215, 2002.

[86] A. Tosoni, P. Capotosto, A. Baldassarre, S. Spadone, and C. Sestieri, "Neuroimaging evidence supporting a dual-network architecture for the control of visuospatial attention in the human brain: a mini review," *Frontiers in Human Neuroscience*, vol. 17, 2023. CC BY 4.0.

[87] C. D. Hacker, T. O. Laumann, N. P. Szrama, A. Baldassarre, A. Z. Snyder, E. C. Leuthardt, and M. Corbetta, "Resting state network estimation in individual subjects," *Neuroimage*, vol. 82, pp. 616–633, 2013.

[88] M. Corbetta, G. Patel, and G. L. Shulman, "The reorienting system of the human brain: from environment to theory of mind," *Neuron*, vol. 58, no. 3, pp. 306–324, 2008.

[89] E. L. Parks and D. J. Madden, "Brain connectivity and visual attention," *Brain connectivity*, vol. 3, no. 4, pp. 317–338, 2013.

[90] T. W. Robbins and B. J. Sahakian, *Attention*, p. 225–232. Cambridge University Press, 2023.

[91] A. A. Sokolov, P. Zeidman, M. Erb, P. Ryvlin, K. J. Friston, and M. A. Pavlova, "Structural and effective brain connectivity underlying biological motion detection," *Proceedings of the National Academy of Sciences*, vol. 115, no. 51, pp. E12034–E12042, 2018.

[92] A. A. Sokolov, M. Erb, A. Gharabaghi, W. Grodd, M. S. Tatagiba, and M. A. Pavlova, "Biological motion processing: The left cerebellum communicates with the right superior temporal sulcus," *NeuroImage*, vol. 59, no. 3, pp. 2824–2830, 2012.

[93] K. Alaerts, S. P. Swinnen, and N. Wenderoth, "Neural processing of biological motion in autism: An investigation of brain activity and effective connectivity," *Scientific reports*, vol. 7, no. 1, p. 5612, 2017.

[94] S. Mojtahedi, "Analyzing effective connectivity of brain using fMRI data: DCM and PPI," Master's thesis, Middle East Technical University, 2013.

[95] C. Büchel and K. J. Friston, "Modulation of connectivity in visual pathways by attention: cortical interactions evaluated with structural equation modelling and fMRI.," *Cerebral Cortex (New York, NY: 1991)*, vol. 7, no. 8, pp. 768–778, 1997.

[96] K. Friston, L. Harrison, and W. Penny, "Dynamic causal modelling," *NeuroImage*, vol. 19, no. 4, pp. 1273–1302, 2003.

[97] E. Raffin, A. Witon, R. F. Salamanca-Giron, K. R. Huxlin, and F. C. Hummel, "Functional segregation within the dorsal frontoparietal network: a multimodal dynamic causal modeling study," *Cerebral Cortex*, vol. 32, no. 15, pp. 3187–3205, 2022.

[98] J. T. Bowling, K. J. Friston, and J. B. Hopfinger, "Top-down versus bottom-up attention differentially modulate frontal–parietal connectivity," *Human brain mapping*, vol. 41, no. 4, pp. 928–942, 2020.

[99] M. Desseilles, S. Schwartz, T. T. Dang-Vu, V. Sterpenich, M. Ansseau, P. Maquet, and C. Phillips, "Depression alters "top-down" visual attention: a dynamic causal modeling comparison between depressed and healthy subjects," *Neuroimage*, vol. 54, no. 2, pp. 1662–1668, 2011.

[100] O. Esteban, C. J. Markiewicz, R. W. Blair, C. A. Moodie, A. I. Isik, A. Erramuzpe, J. D. Kent, M. Goncalves, E. DuPre, M. Snyder, *et al.*, "fMRIPrep: a robust preprocessing pipeline for functional MRI," *Nature methods*, vol. 16, no. 1, pp. 111–116, 2019.

[101] K. Gorgolewski, C. D. Burns, C. Madison, D. Clark, Y. O. Halchenko, M. L. Waskom, and S. S. Ghosh, "Nipype: a flexible, lightweight and extensible neuroimaging data processing framework in python," *Frontiers in neuroinformatics*, vol. 5, p. 13, 2011.

[102] W. D. Penny, K. J. Friston, J. T. Ashburner, S. J. Kiebel, and T. E. Nichols, *Statistical parametric mapping: the analysis of functional brain images*. Elsevier, 2011.

[103] T. M. Inc., "Matlab version: 9.11.0 (r2021b)," 2021.

[104] M. Brett, J.-L. Anton, R. Valabregue, J.-B. Poline, *et al.*, "Region of interest analysis using an SPM toolbox," in *8th international conference on functional mapping of the human brain*, vol. 16, p. 497, Sendai, 2002.

[105] J. Mazziotta, A. Toga, A. Evans, P. Fox, J. Lancaster, K. Zilles, R. Woods, T. Paus, G. Simpson, B. Pike, *et al.*, "A probabilistic atlas and reference system for the human brain: International consortium for brain mapping (ICBM)," *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, vol. 356, no. 1412, pp. 1293–1322, 2001.

[106] J. Mazziotta, A. Toga, A. Evans, P. Fox, J. Lancaster, K. Zilles, R. Woods, T. Paus, G. Simpson, B. Pike, *et al.*, "A four-dimensional probabilistic atlas of the human brain," *Journal of the American Medical Informatics Association*, vol. 8, no. 5, pp. 401–430, 2001.

[107] R. M. Umarova, D. Saur, S. Schnell, C. P. Kaller, M.-S. Vry, V. Glauche, M. Rijntjes, J. Hennig, V. Kiselev, and C. Weiller, "Structural Connectivity for Visuospatial Attention: Significance of Ventral Pathways," *Cerebral Cortex*, vol. 20, pp. 121–129, 04 2009.

[108] P. G. Allan, R. G. Briggs, A. K. Conner, C. M. O'Neal, P. A. Bonney, B. D. Maxwell, C. M. Baker, J. D. Burks, G. Sali, C. A. Glenn, and M. E. Sughrue, "Parcellation-based tractographic modeling of the dorsal attention network," *Brain and Behavior*, vol. 9, no. 10, p. e01365, 2019.

[109] A. S. Greenberg, T. Verstynen, Y.-C. Chiu, S. Yantis, W. Schneider, and M. Behrmann, "Visuotopic cortical connectivity underlying attention revealed with white-matter tractography," *Journal of Neuroscience*, vol. 32, no. 8, pp. 2773–2782, 2012.

[110] R. B. Mars, S. Jbabdi, J. Sallet, J. X. O'Reilly, P. L. Croxson, E. Olivier, M. P. Noonan, C. Bergmann, A. S. Mitchell, M. G. Baxter, T. E. J. Behrens, H. Johansen-Berg, V. Tomassini, K. L. Miller, and M. F. S. Rushworth, "Diffusion-weighted imaging tractography-based parcellation of the human

parietal cortex and comparison with human and macaque resting-state functional connectivity," *Journal of Neuroscience*, vol. 31, no. 11, pp. 4087–4100, 2011.

[111] M. V. Peelen and P. E. Downing, "The neural basis of visual body perception," *Nature reviews neuroscience*, vol. 8, no. 8, pp. 636–648, 2007.

[112] J. A. Pyles and E. D. Grossman, "Neural Mechanisms for Biological Motion and Animacy," in *People Watching: Social, Perceptual, and Neurophysiological Studies of Body Perception*, Oxford University Press, 12 2012.

[113] M. A. Giese and G. Rizzolatti, "Neural and computational mechanisms of action processing: interaction between visual and motor representations," *Neuron*, vol. 88, no. 1, pp. 167–180, 2015.

[114] R. Wang, X. Lu, and Y. Jiang, "Distributed and hierarchical neural encoding of multidimensional biological motion attributes in the human brain," *Cerebral Cortex*, vol. 33, pp. 8510–8522, 04 2023.

[115] K. E. Stephan, W. D. Penny, R. J. Moran, H. E. den Ouden, J. Daunizeau, and K. J. Friston, "Ten simple rules for dynamic causal modeling," *Neuroimage*, vol. 49, no. 4, pp. 3099–3109, 2010.

[116] R. Desimone and J. Duncan, "Neural mechanisms of selective visual attention," *Annual review of neuroscience*, vol. 18, no. 1, pp. 193–222, 1995.

[117] T. Moore and M. Zirnsak, "Neural mechanisms of selective visual attention," *Annual review of psychology*, vol. 68, pp. 47–72, 2017.

[118] E. T. Rolls, G. Deco, C.-C. Huang, and J. Feng, "Multiple cortical visual streams in humans," *Cerebral Cortex*, vol. 33, pp. 3319–3349, 07 2022.

[119] K. E. Stephan, L. Kasper, L. M. Harrison, J. Daunizeau, H. E. den Ouden, M. Breakspear, and K. J. Friston, "Nonlinear dynamic causal models for fMRI," *Neuroimage*, vol. 42, no. 2, pp. 649–662, 2008.

[120] L. Pessoa, S. Kastner, and L. G. Ungerleider, "Neuroimaging studies of attention: from modulation of sensory processing to top-down control," *Journal of Neuroscience*, vol. 23, no. 10, pp. 3990–3998, 2003.

[121] H. Peuskens, J. Vanrie, K. Verfaillie, and G. A. Orban, "Specificity of regions processing biological motion," *European Journal of Neuroscience*, vol. 21, no. 10, pp. 2864–2875, 2005.

[122] J. Herrington, C. Nymberg, S. Faja, E. Price, and R. Schultz, "The responsiveness of biological motion processing areas to selective attention towards goals," *Neuroimage*, vol. 63, no. 1, pp. 581–590, 2012.

[123] P. Zeidman, A. Jafarian, M. L. Seghier, V. Litvak, H. Cagnan, C. J. Price, and K. J. Friston, "A guide to group effective connectivity analysis, part 2: Second level analysis with PEB," *NeuroImage*, vol. 200, pp. 12–25, 2019.

[124] J. Jastorff, R. O. Abdollahi, F. Fasano, and G. A. Orban, "Seeing biological actions in 3D: An fMRI study," *Human Brain Mapping*, vol. 37, no. 1, pp. 203–219, 2016.

[125] B. A. Urgen and A. P. Saygin, "Predictive processing account of action perception: Evidence from effective connectivity in the action observation network," *Cortex*, vol. 128, pp. 132–142, 2020.

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