

NEURAL UNDERPINNINGS OF BIOLOGICAL MOTION PERCEPTION UNDER ATTENTIONAL LOAD

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

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ABSTRACT

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Humans can detect and differentiate biological motion from non-biological motion stimuli effortlessly, even if the stimuli were shown as simplistic as a composition of moving dots (i.e. point-light displays [PLD]). Considering its survival and social significance, BM perception is assumed to occur automatically. Indeed, Thornton and Vuong [1] showed that task-irrelevant BM in the periphery interfered with task performance at the fovea. However, the neural underpinnings of this bottom-up processing of BM lacks thorough examination in the field. Under selective attention, BM perception is supported by a network of regions including the occipito-temporal, parietal, and premotor cortices. A retinotopy mapping study on BM showed distinct maps for its processing under and away from selective attention [2]. Based on these findings, we investigated how bottom-up perception of BM would be processed under attentional load when it was shown away from the focus of attention as a task-irrelevant stimulus. Participants (N=31) underwent an fMRI study in which they performed an attentionally demanding visual detection task at the fovea while intact or scrambled PLDs of BM were shown at the periphery. Our results showed the main effect of attentional load in fronto-parietal regions; as well as, the main effect of peripheral stimuli in occipito-temporal cortex. Both univariate and multivariate pattern analysis results support the attentional load modulation on BM. Lastly, ROI results on each core node of BM processing network expanded these findings by showing that the attentional load modulation on both intact and scrambled BM stimuli were the strongest in bilateral occipito-temporal regions as compared to parietal and premotor cortices. In conclusion, BM was processed within the motion sensitive regions in the occipito-temporal cortex when shown away from the selective attention, and was modulated by attentional load.

Keywords: Biological motion, action perception, point-light displays, attentional load, fMRI, MVPA.



ÖZET

BİYOLOJİK HAREKET ALGISININ DİKKAT YÜKÜ ALTINDA N ÖRAL OLARAK İŞLENMESİ

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Yalnızca hareket eden noktalar halinde (Nokta ışıklı uyaran) gösterilse dahi insanlar biyolojik hareketi (BH) kolayca tespit edip, biyolojik olmayan hareketten çabasızcay ayırt edebilirler. Yaşamsal ve sosyal önemi göz önüne alınarak BH algısının otomatik gerçekleştiği öne sürülmektedir. Öyle ki Thornton ve Vuong [1], çeperdeki görevle ilgisi olmayan BH uyarınının foveadaki performansı etkilediğini göstermiştir. Ancak bu aşağıdan yukarıya gerçekleşen BH işlenmesinin nöral temeli alanda detaylıca incelenmemiştir. Seçici dikkat altında BH algısı, oksipito-temporal, parietal, ve premotor korteksleri içeren bir ağ tarafından desteklenmektedir. BH üzerine yapılan bir retinotopi çalışmasında [2], seçici dikkat altında ve dışında BH için farklı retinotopi haritalandırılması bulunmuştur. Bu sonuçlardan yola çıkarak, dikkat odağının dışında, görevle ilişkisiz olarak çeperde gösterilen BH'nin aşağıdan yukarıya olan algılanmasının dikkat yükü altında nasıl gerçekleştiğini araştırdık. Katılımcılar (N=31), foveada dikkatlerini vermeleri gerektiği bir görsel tespit deneyini yaparlarken çeperde düzgün ya da karıştırılmış BH uyarını gördükleri iMRG çalışmamıza girdiler. Sonuçlarımız dikkat yükünün ana efektini fronto-parietal bölgelerde, çeperdeki uyarıların ana efektini ise oksipito-temporal kortekste gösterdi. Hem tek-değişkenli hem de çok değişkenli örüntü analizi sonuçları BH üzerindeki dikkat yükü modülasyonunu desteklemektedir. Ayrıca, BH algısını destekleyen temel bölgeleri ilgi bölgesi olarak seçtiğimiz analiz de sonuçlarımızı detaylandırarak dikkat yükünün BH üzerindeki etkisinin bilateral oksipito-temporal kortekste parietal ve premotor korteks bölgelerine göre daha güçlü olduğunu gösterdi. Sonuç olarak, seçici dikkat dışında BH, harekete duyarlı oksipito-temporal korteks bölgelerince işlenmiş ve dikkat yükü tarafından modüle edilmiştir.

Anahtar sözcükler: Biyolojik hareket, eylem algısı, nokta-ışıklı görüntü, dikkat yükü, iMRG, çok değişkenli örüntü analizi.

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Contents

1	Introduction	1
1.1	Point-light Displays of Biological Motion	1
1.2	Neural Processing of Biological Motion	3
1.3	Top-down and Bottom-up Perception of Biological Motion	6
1.4	Attentional Load	9
1.5	Current Study	11
2	Methods	13
2.1	Participants	13
2.2	Stimuli and Apparatus	13
2.3	Experimental Design	15
2.4	Data Collection and Acquisition	18
2.5	Behavioral Data Analysis	18
2.6	fMRI Data Preprocessing and Statistical Analyses	19

2.6.1	Anatomical and Functional Data Preprocessing via fMRIPrep	19
2.6.2	Whole-brain fMRI Analyses	22
2.6.3	ROI Analyses	24
3	Results	26
3.1	Behavioral Results	26
3.1.1	Accuracy	26
3.1.2	Reaction Times	26
3.2	Whole-brain Analyses	27
3.2.1	Univariate Results	28
3.2.2	Searchlight based MVPA	32
3.3	ROI Analyses	35
3.3.1	Univariate ROI Results	37
3.3.2	Multivariate ROI Results	39
4	Discussion	46
4.1	The Bottom-up Perception of BM: Recruited Regions	47
4.2	Engagement of Top-down and Bottom-up Attention Networks . .	49
4.3	Limitation	50
4.4	Future Directions	51

4.5 Conclusion	52
A High versus Low Attentional Load Decoding Results	65
B DMN and FPN Regions under Low >High and High >Low Contrasts	66
C Permissions to Re-use Figures	68

List of Figures

1.1	Static image representation of an actor and his PLD . . .	2
1.2	Brain regions and their associated roles during BM perception	4
2.1	Stimuli design and procedure	16
2.2	ROI masks shown on the inflated brain	24
3.1	Reaction times	28
3.2	The activity maps of the main effect of attentional load .	29
3.3	The activity maps of the High >Low attentional load t-contrast	30
3.4	The activity maps of the Low >High attentional load t-contrast	31
3.5	The activity maps of the main effect of peripheral stimulus	32
3.6	The activity maps of the BM >None t-contrast	33
3.7	The activity maps of the SCR >None t-contrast	34

3.8	Decoding regions of the BM versus None classification . .	35
3.9	Attentional load modulation on BM	36
3.10	Decoding regions of the SCR versus None classification .	37
3.11	Attentional load modulation on SCR	38
3.12	Beta values across BM and SCR >None conditions	40
A.1	High versus Low Attentional Load Decoding Results . . .	65
B.1	DMN and FPN Regions under Low >High and High >Low Contrasts	67

List of Tables

3.1	Main effect of attentional load. Results were FWE-corrected, at a threshold of $p < .05$	41
3.2	Main effect of peripheral stimulus. Results were at an uncorrected threshold of $p < .001$	42
3.3	Attentional load modulation on peripheral stimulus. Results were at an uncorrected threshold of $p < .001$	43
3.4	Attentional load modulation on BM indicated by the diminished extent of decoding regions. Results were FWE-corrected, at a threshold of $p < .05$	44
3.5	Univariate Distractor Contrasts within inclusive ROI masks. Results were FWE-corrected, at a threshold of $p < .05$	44
3.6	MVPA Distractor Comparisons within inclusive ROI masks. Results were FWE-corrected, at a threshold of $p < .05$	45

Chapter 1

Introduction

In a crowded street, with lots of people passing by, attentively or inattentively we perceive most of these passengers fallen in our sight. With just a glance of an eye, humans can detect and differentiate biological motion from non-biological motion stimuli easily, even if the stimuli were shown as simplistic as a composition of moving dots (i.e. point-light displays [PLD]).

1.1 Point-light Displays of Biological Motion

By definition, any movement performed by an organism is called biological movement. Conventionally, biological motion (BM) is the term used for action perception research. Recognition and understanding of BM is crucial for identifying if the observed organism is a predator, a prey, or a mate [3, 4]. In order to study BM perception, in addition to the static images, dynamic videos, and rendered animations; PLDs of BM are frequently used in the literature. Starting with the early research of Johansson [5], PLDs were constructed as follows: an actor in front of a dark background who is wearing a dark suit with light sources attached onto his joints is captured as he performs a certain action (e.g. walking, jumping, crawling etc.) (Figure 1.1). Nowadays, with the advancement of

technology, there are open databases for BM researchers to select a PLD of their interest among various actions that were performed by many actors and actresses (e.g. <http://mocap.cs.cmu.edu/motcat.php>).

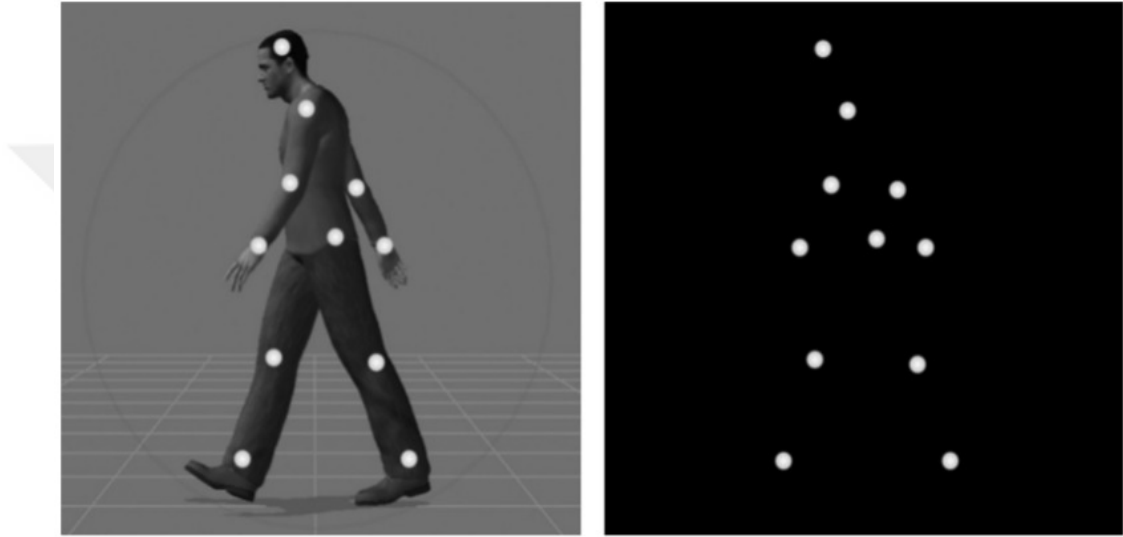


Figure 1.1: **Static image representation of an actor and his PLD.** A total of 13 dots visible on the head and joints of the actor is shown[6]. Each dot was anchored to the corresponding joint. In this lateral view, only one shoulder and one hip joint is visible. Reprinted with permission from Thompson (2015, pp. 428).

What is evident in this display is that if the captured video is shown as a static, single frame image, no meaningful information regarding BM can be inferred. However, once the frames are shown in subsequent order, the form and motion features of the acted BM can be well understood [6]. This nature of PLDs provides two main advantages to researchers. First of all, PLDs are easy to manipulate. One can disrupt the form and motion features of the PLD animation either together or separately in both space and time. For instance, by scrambling the anchor points of the PLD, one can disrupt the form information. Also, as the time interval between PLD frames increases, the motion information gets distorted. Moreover, adding noise masks to the PLD stimuli or changing the contrast of the dots decreases the overall understanding of the form information [7]. The second advantage is that PLDs control for form-related confounds such as color,

texture, and shape. Unlike with the use of natural videos, researchers avoid any unnecessary information related with the background scene or the object-related features that is observable from the action movie [8]. Thus, PLDs are advantageous in terms of the ease of manipulation and avoiding confounds.

1.2 Neural Processing of Biological Motion

According to Thompson and Parasuraman [9], BM perception requires three main steps: (1) Detecting the features that constitute body movements, (2) forming action specific representations, and (3) understanding intentions from observed actions. These steps are supported by a network of regions including form and motion sensitive areas in the occipito-temporal cortex (OTC) that encodes visual features; an integrative hub at superior temporal sulcus (STS) that creates action representations; and finally parietal and frontal regions such as inferior parietal lobule (IPL), anterior intraparietal sulcus (aIPS), inferior frontal gyrus (IFG) and premotor cortex (PMC) that are important for understanding the meaning of actions as well as processing the intentional and goal-oriented behavior Figure(1.2).

The first step of BM perception follows the two-visual pathway hypothesis [10]. Accordingly, as indicated by the results of early lesion studies with non-human primates, there are two pathways within the brain that processes visual information. The ventral pathway (i.e. the “what” pathway) encodes form-related features of the perceived visual object; whereas, the dorsal pathway (i.e. the “where” pathway) encodes the motion-related features. They both stem from the early visual cortex and start from extrastriate areas to the lateral and inferior temporal lobe along the ventral; and fronto-parietal regions along the dorsal pathway [11]. In terms of BM perception, the form and motion information is processed within the inferior temporal cortex (ITC) including inferior temporal sulcus (ITS) and inferior temporal gyrus (ITG); as well as ventral (VT) and middle temporal (MT) cortex regions[12]. Specifically, the body form information is processed within the extrastriate body area (EBA). Regardless of the stimuli

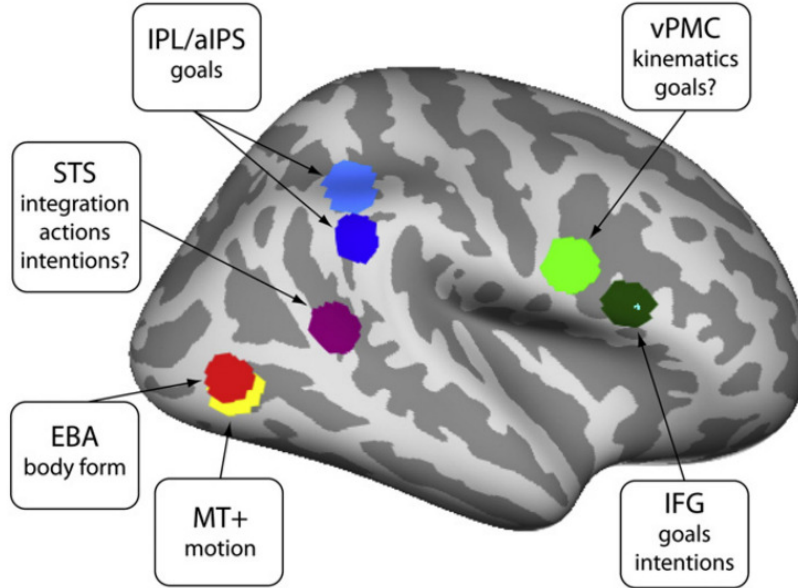


Figure 1.2: **Brain regions and their associated roles during BM perception.** A network of regions including occipito-temporal, parietal, and premotor cortices supports the perception of BM[9]. Reprinted with permission from Thompson and Parasuraman (2012, pp. 6).

being static or dynamic [13, 14, 15, 16], it's been found that EBA prefers intact PLDs of BM over scrambled counterparts, and shows strong selectivity towards human body and BM stimuli [16]. Furthermore, it's been suggested that EBA may integrate motion and form cues [15, 16]. This is not surprising considering that EBA overlaps with the motion sensitive human MT cluster (hMT+) [17, 18, 19]. Interestingly, although hMT+ activity is higher towards intact PLDs of BM compared to scrambled controls, for almost every complex motion pattern including biological and 3D geometric shapes, hMT+ activity is observed [18]. Thus, it can be said that rather than BM specific motion encoding, hMT+ is associated with motion patterns [14, 20, 18]. In addition to EBA and hMT+, there is another area that is important for processing the low-level features of BM: fusiform body area (FBA). It is a body-specific area in the ventral parts of ITC. Unlike EBA, FBA is selective towards stationary body figures [21]. This suggests that FBA may be extracting the body shape and posture information from BM [22, 23, 16], even from the intact PLD stimuli [24, 14, 25]. In sum, the visual features of BM are processed within the form sensitive EBA and FBA

regions, as well as the motion sensitive hMT+.

The second step of BM perception occurs within the STS. It is the most prominent region that has been studied in the BM literature [12]. Anatomically and functionally, the STS seems to be a convergent point of dorsal and ventral visual pathways [26]. Thus, it is considered to be the integration hub for motion and form information that creates action representations [27, 28, 29]. Also, it was found that STS showed increased activity towards intact PLDs of BM as compared to coherent dot motion or scrambled BM stimuli [14]. This finding is in line with the neurophysiological evidence from macaque monkeys that shows BM-selective neurons in the STS [30]. Furthermore, in addition to the encoding and integration of visual features [31, 32], STS is also related with the processing of more abstract properties of the observed action. Separate neuron populations for encoding visual and more abstracted properties of an observed action were evident in the macaque STS [33]. The human studies also show consistent evidence that STS processes the abstract representations of actions even when they were imagined [34, 35] or parts of arbitrary social interaction [36, 37]. Based on these findings, a functional organization within the human STS could be possible [38, 39, 40]. Thus, in terms of BM perception, STS is a BM-selective region that was found to be related with the integration of visual features, as well as the processing of abstract properties of the observed action. Starting with the STS, BM perception involves not only action perception but also action understanding [41].

The final step of BM perception involves fronto-parietal regions that are evident in the action understanding literature [8]. In the early electrophysiology studies on macaque monkey brains, these regions have been identified as parts of the mirror neuron system [8]. Accordingly, mirror neurons are visuo-motor neurons within the F5 area of the macaque PMC that fires during action execution, as well as the observation of another agent's action [42]. Furthermore, similar response patterns were evident in the parietal cortex such that both the premotor and the parietal mirror neuron regions yielded somatotopic organization [43]. Human studies on action observation yield similar functional division in the parietal and premotor cortices [44]. While the functional organization in the

parietal cortex is based on the overall goal of the action [45, 46]; effector-specific functional organization is evident in the PMC [47, 46, 48]. Thus, unlike OTC regions that encode the visual features of BM, fronto-parietal areas are important for understanding the goal and the kinematics of the observed action.

Overall, the BM perception is supported by form and motion sensitive regions within the OTC including STS as the integration hub that forms abstract action representations, as well as the fronto-parietal regions that are associated with the action understanding. This network of regions is consistently evident in the literature that studied the BM stimuli under selective attention. However, considering the innate tendency and social interference ability of humans towards the BM stimuli, BM perception can be assumed to occur automatically in an effortless manner [5, 9, 49, 1]. In such bottom-up processing, distinct regions in this aforementioned network are found to be activated.

1.3 Top-down and Bottom-up Perception of Biological Motion

Early models of BM processing based on neurophysiological data of humans and macaque monkeys [50, 17] relied on bottom-up processing of BM. Accordingly, the visual features are encoded separately in a hierarchical manner along the motion and form-sensitive pathways up until the STS. In these models, the role of top-down modulations was overlooked and no feedback projection was defined. However, in an early study [49], it was shown that when the BM perception was disrupted, attentional resources were required to process BM through top-down processing. Later studies following this work consistently showed that despite its robustness, BM perception is modulated by attention and other top-down factors. These factors are evident when the BM stimulus is under non-optimal conditions such as it is either degraded, ambiguous, or superimposed onto one-another [51]. Furthermore, higher level understanding of actions also demands recruitment of attentional resources [52, 53].

Thus, unlike early models, current studies show that both top-down and bottom-up processing of BM are apparent. However, there is not much study in the literature that examines the interaction and the relationship between these two mechanisms. In order to conduct such studies, a research paradigm that separates top-down and bottom-up modulations is required. This is possible via directing participants' selective attention at a main task while showing BM stimuli at another location (e.g. periphery). By doing so, the top-down resources such as selective attention would be allocated at the fixation on the main central task; and it would be possible to observe if the peripheral stimulus is processed in a bottom-up manner. Then, for instance, if the main task performance at fixation is affected by the peripheral stimulus, it can be concluded that peripheral stimulus was processed in a stimulus-driven manner. Interestingly, there is not much study in the field that successfully applied this paradigm. One example study that showed the effect of bottom-up processing of BM on the main task performance was conducted by Thornton and Vuong [1]. They have adapted a Flanker task [54] in which three BMs were shown at the center of the screen. The one in the middle was the target stimulus, whereas the other two were flankers. They have found that when the walking direction of the flanker PLDs of BM were incongruent with that of the target, participants' performance was worse than the congruent situation. Thus, it was shown that although the focus of attention was directed at the foveal target, the "to-be-ignored" task-irrelevant BM stimuli in the periphery affected the main task performance. Authors concluded that with this study, they have shown the incidental processing of BM stimuli. A similar study was conducted by Ikeda, Watanabe and Cavanagh [55]. Researchers displayed three PLDs of BM stimuli at the periphery in which two of them were Flankers. Participants had to discriminate the walking direction of the stimulus in the middle of the triplet while they were fixating at the fovea. It was found that, as the distance between stimuli decreased, the crowding effect occurred and the performance was disrupted. More interestingly, when the flankers were scrambled PLDs of BM, there was no effect of crowding even though the distance between pairs was as little as two visual degrees. Thus, this study shows that even when participants did not overtly direct their attention to the periphery, BM stimuli were perceived automatically, and participants could discriminate

scrambled PLDs from intact ones.

The neuroimaging studies on the top-down and the bottom-up perception of BM can be summarized into those that applied active versus passive viewing tasks with the PLDs of BM stimuli. The difference between these two tasks is the allocation of the focus of selective attention. By definition, selective attention is our ability to focus on the task at hand while avoiding the task-irrelevant stimuli. Accordingly, during passive viewing tasks, participants are engaged in a main task that is irrelevant to BM perception such that their attention is directed away from the BM stimuli. In these tasks, the bottom-up processing of BM can be examined. However, during active viewing tasks, participants are asked to execute a main task on the BM stimulus such that the attentional focus is directed at the BM. Thus, top-down resources are available for BM perception.

In terms of active processing of BM, Saygin and colleagues [41] conducted a study in which participants were asked to indicate whether the color of PLDs were green or not in each trial. They found intact BM related activity across OTC including STS as well as fronto-parietal regions such as IPS, IFG and ventral PMC. This study was first to find frontal activation towards PLDs of BM. However, in the studies that adopted passive viewing task, the activity maps include the visual feature encoding areas (i.e. EBA, hMT+, FBA) up until STS. For instance, in one study [15], when participants passively viewed the PLDs of a walking human motion, only the occipital and ventral temporal areas (i.e. EBA, hMT+) showed significant activation. When the researchers asked participants to adopt a one-back task (i.e. responding whether the subsequent trials are of the same stimulus); thus, when participants were engaged in active processing of BM stimuli, STS and IFG activations were observed. Moreover, Safford and colleagues [56] specifically examined the attentional modulation on the BM processing area STS and found that on a display of superimposed point-light figures of BM and tool motion, the STS activity was suppressed when the participants attended to the tool motion rather than the BM. Thus, this finding shows directly that the STS activity is modulated by selective attention. In another study that manipulated the modulation of selective attention on BM processing, Herrington

and colleagues [4] compared passive color detection versus active goal understanding task on PLDs of BM stimuli. They found that right anterior STS, as well as hMT+ and EBA activations were stronger in goal understanding compared to the color detection task. Finally, in a retinotopy study that examined BM processing under active or passive viewing conditions, Saygin and Sereno [2] showed a wedge consisting of three BM stimuli in front of a background that contains either scrambled or intact PLDs of BM. When participants were engaged in an active task on BM stimulus, retinotopic maps were observed in VTC, lateral occipital cortex (LOC), hMT+, STS, IPS, posterior parietal cortex (PPC), and superior precentral sulcus (i.e. frontal eye field [FEF]). Meanwhile, during the passive viewing task, the activity found in all these regions were either reduced or diminished such that only OTC regions (V3, hMT+, LOC, STS) and IPS yielded retinotopic maps.

Overall, based on these findings, it can be concluded that the occipito-temporal regions including extrastriate and inferotemporal cortex areas (i.e. EBA, hMT+, FBA) process the form and motion features of the BM stimulus automatically, while the STS and fronto-parietal activity requires active processing. Although these studies' findings are informative, because they separated active and passive viewing conditions in different blocks, the interaction between the top-down and bottom-up processing of BM perception cannot be observed. A single experimental condition that executes both of these mechanisms is needed. One such paradigm to study the bottom-up perception of BM while examining its modulation under a top-down mechanism could be attentional load.

1.4 Attentional Load

Load theory proposed by Lavie [57, 58] suggests that successful filtering of the irrelevant stimulus depends on the attentional load of the task at hand. This proposal is based on the assumption that perception has a limited capacity such that one cannot process every single stimulus in the environment. Attention works as a regulatory mechanism to focus on what is relevant, salient, or important for

processing, and filter out the rest. If the attentional or perceptual load of the task is high, then there is no capacity left for task-irrelevant stimuli to interfere; however, if the load is low, then there is processing capacity left for interference. This rather abstract proposal was supported by a recent study on cellular metabolism [59]. By measuring oxidation levels of a cellular metabolism marker with broadband near-infrared spectroscopy, it was found that regardless of the mental processing demands, overall cerebral energy supply was constant. Thus, it can be concluded that attention worked as a compensatory mechanism to regulate the cellular metabolism levels based on the trade-off between the processing demands of the task and the irrelevant stimulus.

Considering the active versus passive viewing tasks that have been studied widely in the BM literature, in the case of a foveal main task with peripheral BM used as a task-irrelevant stimulus, the modulation of the active mechanism (i.e. attentional load modulation) would be evident on the passive processing of BM stimuli. Therefore, the relationship between the bottom-up and top-down processing of BM stimulus can be observed through a single task. Similarly, a typical attentional load study is designed as follows: an irrelevant stimulus is presented at the periphery, while participants are enrolled in a visual detection task that demands either high or low attention at the fovea. In accordance with the load theory assumptions, the activation related to the unattended stimuli is stronger in low attentional load conditions, while it is decreased or diminished in the high load. To date, flickering checkerboards, optic flow of lines, and colorful patches have been used as irrelevant peripheral stimuli, and processing of these stimuli has been found to be modulated by attentional load at early visual cortex areas (V1-V4), motion sensitive MT cortex, and color responsive area V4, respectively [60, 61, 62]. For instance, in the retinotopy study conducted by Schwartz and colleagues [62], while participants were engaged in a visual detection task at the center, a flickering checkerboard was shown at the periphery in half of the trials. Their results showed that throughout the early visual cortex regions up until V4, the activation related with the task-irrelevant checkerboards was significantly lower in the high load compared to the low load conditions. This difference was

stronger in V4 compared to V1. Similarly, in the very first attentional load neuroimaging study, Rees [61] asked participants to detect the word either starting with an uppercase letter (i.e. low load) or that is bi-syllable (i.e. high load). While they were engaged in that task, optic flow of lines were shown on the rest of the field of view. It was found that during the high load condition, MT activation corresponding with the optic flow processing was significantly diminished compared to low attentional load block. Chong and colleagues [63] have adopted a similar study as that of Rees [61]. Rather than an optic flow of lines, a movie of a hand-grasping action was shown in the background while participants were engaged in an attentional load task at the center (i.e. discriminating a gap between lines in a diamond figure). Among their regions of interest (IFG, IPL, STS, supramarginal gyrus), they have found a significant attentional load modulation in right IPL and left IFG.

Based on these studies, conducting an attentional load experiment while displaying PLDs of BM as task-irrelevant peripheral stimuli would fill the gap in the BM perception literature by showing the neural underpinnings of the interaction between top-down and bottom-up processing of BM. This interaction would be evident by the differences in the activity maps that are observed across attentional load conditions. Activity changes related with both stimulus-driven processing of task-irrelevant BM and the top-down modulation of selective attention on its processing can be observed.

1.5 Current Study

In this current study, we have adopted a main visual detection task at the fovea that has been widely used in the literature [62, 64, 60, 59]. The main task was either accompanied by an intact or a scrambled PLD of BM that was displayed unilaterally in the periphery or there was no peripheral stimulation at all. By applying the attentional load paradigm, our aim was to answer these two questions: (1) whether BM would be processed when it is shown away from the focus of attention as a task-irrelevant peripheral stimulus, and (2) if so, whether

BM processing would be modulated by attentional load. By answering these questions, we can show (1) if BM is automatically processed in a bottom-up manner, even when selective attention is not directed towards it; and (2) whether this bottom-up processing is modulated by a top-down factor that is attentional load. Thus, with this study design, we can examine the relation between bottom-up and top-down processing of BM in a single task.

Considering the previous literature on the neural correlates of BM processing [15, 2, 9], we have hypothesized that:

(1) BM stimulus would be processed in a bottom-up manner even if it was shown away from the focus of attention.

(2) Visual feature encoding regions (i.e. hMT+, EBA) and possibly the higher level regions such as STS and fronto-parietal cortex areas (i.e. IPS, PMC) would be activated in the intact BM condition.

(3) The activation related to both intact and scrambled BM conditions would be modulated by attentional load.

Chapter 2

Methods

2.1 Participants

31 healthy volunteers (23 female; age range 18-31, mean age 23.05) participated in the study. All participants had normal or corrected-to-normal visual acuity and no long-term use of medication for a neurological or psychiatric disorder. The study was approved by the Human Research Ethics Committee of Bilkent University and all volunteers gave written informed consent and filled the pre-screening form prior to the experiment. After the experiment, each participant received 50 TL as compensation.

2.2 Stimuli and Apparatus

There were two kinds of stimulus display presented onto the screen: (1) T-shaped stimuli shown at the fovea; (2) PLDs of intact or scrambled BM stimulus shown at the periphery. All stimuli were generated and presented by using the Psychophysics Toolbox (Psychtoolbox Version 3 [PTB-3]) [65, 66, 67] and BioMotion Toolbox [68] running under MATLAB (The Mathworks, Natick, MA)

to obtain precise timing and visualization.

During the main experiment, participants engaged in a visual detection task on a stream of rapid serial visual presentation (RSVP) of t-shaped stimuli shown at the fixation. The task was adapted from previous neuroimaging studies that examined the modulation of attentional load [62, 60, 64, 59]. The RSVP task consisted of two pseudorandom series of six t-shaped stimuli varying in their color (red, green or yellow) and orientation (upright or upside-down); comprising a total of twelve shapes per task. Stimulus displays across attentional load blocks were the same, while the instruction screens differed. Depending on the task instruction, participants had to give a button-response to a target stimulus. The participants' response was collected with a fiber optic response box (Current Design, fORP 904 fMRI trigger and response system). The number of target stimuli (four out of twelve) and overall t-shape displays were kept the same in each RSVP task throughout the experiment regardless of the task instruction. Each t-shaped stimulus was shown for 500 ms with a subsequent interstimulus interval ranging between 250 and 350 ms (Figure 2.1.A). The foveal t-shaped stimulus stream was shown continuously with or without a distractor shown at the periphery throughout an experimental block and each randomly ordered experimental block lasted 10 seconds.

In addition to the foveal t-shaped stimuli, on some of the experimental trials, there were point-light displays (PLDs) of either intact or scrambled BM stimulus shown at the right or the left side of the main task, 4 degrees away from the fixation (Figure 2.1.B). The PLD animation of a walking human was downloaded from Carnegie Mellon University's motion capture database (CMU Graphics Lab, <http://mocap.cs.cmu.edu/>). The stimulus was edited by using Motion Kinematic and Kinetic Analyser software (MOKKA, 2018, <https://biomechanical-toolkit.github.io/mokka/>) in order to acquire a 2D stimulus having a "towards-looking" position from its initial 3D shape, and to comprise of a total of 13 dots shown at the head, and bilateral shoulders, elbows, hands, waist bones, knees, and feet joint locations. The stimulus cycle was reduced to one second and consisted of 61 frames. The scrambled motion stimulus (SCR) was used as a control for the intact BM. It was created via BioMotion Toolbox [68] by shuffling the

anchor positions of dots in the intact BM stimulus while keeping each dot's local motion trajectories the same. Therefore, SCR had the same number of dots, and the same local dot motion as in intact BM; whereas, the global form and motion of the intact BM was disrupted in SCR.

2.3 Experimental Design

The experiment consisted of eight runs. Each run included four rest and three pairs of experimental blocks. In rest blocks, participants were asked to fixate on a cross shown at the fovea for 11 seconds. The experimental blocks were shown as subsequent pairs (Figure 2.1.C). They started with either the high or low attentional load instruction screen (Figure 2.1.D). The order of which attentional load block comes first was counterbalanced. Each experimental block consisted of six peripheral stimulation conditions that were randomized in their order: BM-right, BM-left, SCR-right, SCR-left, No-peripheral-stimulus condition (None). The None condition was shown twice, in order to equalize the number of each peripheral condition.

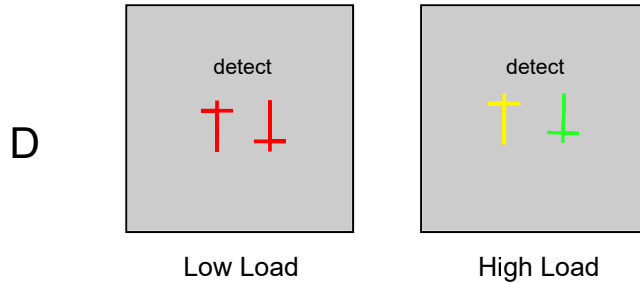
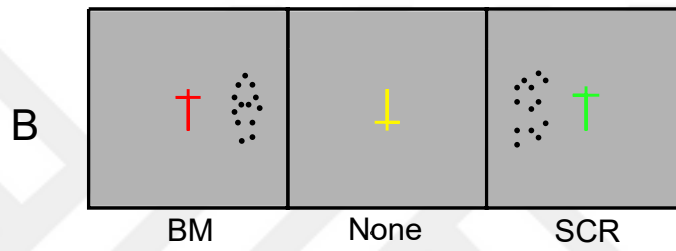
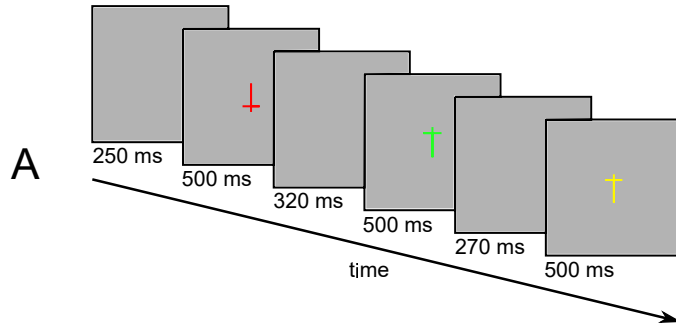


Figure 2.1: Stimuli design and procedure. Participants were engaged in a visual detection task at the fovea. (A) T-shape like figures varying in their color (i.e. red, green, yellow) and orientation (i.e. upright, upside-down) were shown for 500 msec followed by inter-stimulus intervals ranging between 250 and 350 msec randomly. (B) An intact (i.e. BM) or a scrambled biological motion stimulus (i.e. SCR) or no stimulus at all (i.e. None) was presented in the periphery. (c) In each run, there were four rest and three pairs of experimental blocks. The display of main task and the task-irrelevant peripheral stimulus was kept the same over each experimental block in all runs. (D) Only the instruction screen differed displaying the target stimuli on the screen. LL: Low load, HL: High load.

Before the MRI session, participants were familiarized with the intact and scrambled BM stimuli by viewing them separately on the laptop screen for twenty seconds each. They were asked to fixate on the animation, while the experimenter articulated the features of each stimulus (i.e. pointing the overall figure of a “walking human” by showing its head, hand swings, and stepping movement for the intact BM; saying “random dot movements with no meaning” for the SCR). Later on, in order to test if participants could differentiate the intact BM stimulus from the SCR shown in the periphery, participants performed a short task in which they were asked to fixate on a cross at the fovea and press the corresponding arrow key on the keyboard when they saw intact BM stimulus on right or left side of the screen. Finally, participants practiced the main task without any distractors for 36 trials for each attentional load condition. They pressed the spacebar to indicate their response. After ensuring that their performance was above 80% they were taken into the scanner room.

During the scanning session, participants performed a visual detection task that is varying in its attentional load based on the given instruction. Participants were told explicitly to focus on giving correct answers for the main task and avoid looking at peripheral distractors. During low attentional load blocks, participants were asked to detect red shapes; for the high attentional load blocks, they had to detect upright yellow and upside-down green t-shapes. This manipulation relies on the study conducted by Schwartz and colleagues [62]. Here, asking participants to detect red shapes depends on the “pop-out” feature of one color among three others; meanwhile, detecting upright yellow or upside-down green t-shapes requires discrimination of a conjunction of color and orientation among all six combinations. Thus, the latter one demands more focused attention compared to the first instruction. Lastly, based on the task instruction, participants’ responses were collected as a button-press on a predetermined key from a fiber optic response box.

2.4 Data Collection and Acquisition

Participants were scanned at National Magnetic Resonance Research Center (UMRAM) in Bilkent University by using 3T Siemens TimTrio MR scanner with a 32-channel phase array head coil. In order to minimize head movement, participants' heads were supported with foam paddings under their skull, around their neck, and under their legs. Also, they were given ear plugs to reduce their exposure to loud scanner noise. Stimuli were presented on an MR compatible 800x600 pixel, 32 inch LCD screen with a 60 Hz refresh rate (For the first 18 participants: TELEMED; and for the last 13 participants: TROYKA MED), and seen through a mirror system mounted on top of the head coil that is 168 cm away.

Before starting the experimental scans, participants' high resolution T1-weighted structural images were obtained (TR=2600 ms, TE=2.92 ms, flip angle=12°, FoV read=256 mm, FoV phase=87.5%, 176 slices with 1×1×1 mm³ resolution). Later on, for each of the eight experimental runs, 227 functional images were acquired using gradient-echo planar imaging (TR=2000 ms, TE=22 ms, flip angle=90°, 64 x 64 matrix, FoV read=192 mm, 43 slices with a thickness of 2.5mm, 3×3×2.5 mm³ resolution).

2.5 Behavioral Data Analysis

A 2 x 3 repeated measures of ANOVA was conducted ($N=31$) to investigate the effect of attentional load (AL: High, Low) and peripheral stimulus (PS: BM, SCR, None) on reaction times and accuracy. P-value was adjusted according to Bonferroni correction for $p < .05$.

2.6 FMRI Data Preprocessing and Statistical Analyses

2.6.1 Anatomical and Functional Data Preprocessing via fMRIPrep

Results included in this thesis come from preprocessing performed using fMRIPrep 20.1.1 [69, 70](RRID:SCR_016216), which is based on Nipype 1.5.0 [71, 72](RRID:SCR_002502).

2.6.1.1 Anatomical data preprocessing

A total of 2 T1-weighted (T1w) images were found within the input BIDS dataset. All of them were corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection [73], distributed with ANTs 2.2.0 [74](RRID:SCR_004757). The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast [75](FSL 5.0.9, RRID:SCR_002823). A T1w-reference map was computed after registration of 2 T1w images (after INU-correction) using mri_robust_template (FreeSurfer 6.0.1)[76]. Brain surfaces were reconstructed using recon-all (FreeSurfer 6.0.1, RRID:SCR_001847)[77], and the brain mask estimated previously was refined with a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle (RRID:SCR_002438)[78]. Volume-based spatial normalization to one standard space (MNI152NLin2009cAsym) was performed through nonlinear registration with antsRegistration (ANTs 2.2.0), using brain-extracted versions of both T1w reference and the T1w template. The following template was selected for spatial normalization: ICBM 152 Nonlinear Asymmetrical template version 2009c[79] [RRID:SCR_008796; TemplateFlow ID:

MNI152NLin2009cAsym],

2.6.1.2 Functional data preprocessing

For each of the 8 BOLD runs found per subject (across all tasks and sessions), the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt (FSL 5.0.9) [80]. BOLD runs were slice-time corrected using 3dTshift from AFNI 20160207 [81](RRID:SCR_005927). Susceptibility distortion correction (SDC) was omitted. The BOLD reference was then co-registered to the T1w reference using bbregister (FreeSurfer) which implements boundary-based registration [82]. Co-registration was configured with six degrees of freedom. The BOLD time-series (including slice-timing correction when applied) were resampled onto their original, native space by applying the transforms to correct for head-motion. These resampled BOLD time-series will be referred to as preprocessed BOLD in original space, or just preprocessed BOLD. The BOLD time-series were resampled into standard space, generating a preprocessed BOLD run in MNI152NLin2009cAsym space. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Several confounding time-series were calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and three region-wise global signals. FD was computed using two formulations following Power (absolute sum of relative motions)[83] and Jenkinson (relative root mean square displacement between affines)[80]. FD and DVARS are calculated for each functional run, both using their implementations in Nipype (following the definitions by Power et al. 2014[83]). The three global signals are extracted within the CSF, the WM, and the whole-brain masks. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (CompCor)[84]. Principal components are estimated after high-pass filtering the preprocessed BOLD time-series (using a discrete cosine filter with 128s cut-off) for the two CompCor

variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 5% variable voxels within a mask covering the subcortical regions. This subcortical mask is obtained by heavily eroding the brain mask, which ensures it does not include cortical GM regions. For aCompCor, components are calculated within the intersection of the aforementioned mask and the union of CSF and WM masks calculated in T1w space, after their projection to the native space of each functional run (using the inverse BOLD-to-T1w transformation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each [85]. Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardized DVARS were annotated as motion outliers. All resamplings can be performed with a single interpolation step by composing all the pertinent transformations (i.e. head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using `antsApplyTransforms` (ANTs), configured with Lanczos interpolation to minimize the smoothing effects of other kernels [86]. Non-gridded (surface) resamplings were performed using `mri_vol2surf` (FreeSurfer).

Many internal operations of fMRIPrep use Nilearn 0.6.2 [87](RRID:SCR_001362), mostly within the functional processing workflow. For more details of the pipeline, see the section corresponding to workflows in fMRIPrep's documentation.

2.6.2 Whole-brain fMRI Analyses

2.6.2.1 Univariate Analysis and Activation Maps

After preprocessing, first-level analysis was conducted by using SPM12 software package (<http://www.fil.ion.ucl.ac.uk/spm/software/spm12/>) running under MATLAB (The Mathworks, Natick, MA). General linear model (GLM) of each subject was run with a design matrix of 14 regressors including six experimental conditions (BM under High Load [HBM], BM under Low Load [LBM], SCR under High Load [HSCR], SCR under Low Load [LSCR], None under High Load [HNone], None under Low Load [LNone]), one fixation block, six motion regressors (three rotations, three translations), and a constant factor. Each regressor was convolved with the default canonical hemodynamic response function used in SPM12.

After completing the first-level analysis, group level analysis was performed as a 2 (AL: High, Low) x 3 (PS: BM, SCR, None) repeated-measures of analysis of variance (ANOVA) using the SPM12 flexible factorial design [88]. Flexible factorial design allows users to test main and interaction effect of interest while considering the variance and dependency measures for sphericity assumptions of experimental and subject effects [89]. In order to run flexible factorial analysis, experimental conditions (AL and PS) and subjects were defined as dependent and independent factors respectively. Each subjects' positive contrasts of each experimental condition were used as input scans for defining the factor analysis structure. No additional parameter and covariant were included.

Linear contrasts tested in the group analysis were based on understanding the main effect of AL and PS conditions separately. Planned t-contrasts were then created to examine the AL effect on each PS condition as well as pairwise comparisons of PS in each AL condition: (1) AL effect on BM: HBM minus LBM; (2) AL effect on SCR: HSCR minus LSCR; (3) AL effect on None: HNone minus LNone; (4) Difference between intact and scrambled BM: BM minus SCR, HBM minus HSCR, LBM minus LSCR; (5) Difference between intact BM and None:

BM minus None, HBM minus HNone, LBM minus LNone; (6) Difference between scrambled BM and None: SCR minus None, HSCR minus HNone, LSCR minus LNone. Each of these t-maps was thresholded to FWE-corrected, $p < 0.05$.

2.6.2.2 Searchlight based Multivoxel Pattern Analysis (MVPA)

We ran several classifiers to discriminate between the conditions of AL as well as the conditions of PS. In order to differentiate the pattern of activation in high and low AL blocks, “High versus Low” binary classification was run across labels. In addition, a three-way PS classification was run including BM, SCR, and None as PS classes. Furthermore, the planned t-contrasts defined at the univariate analyses were used as pairwise discriminations to examine the modulation of AL on PS.

A linear support vector machine (LibSVM; regularization parameter $C = 1$) was performed via the Decoding Toolbox [90] using searchlight method. Runwise beta images were extracted from GLM and used as input for the classifiers. Leave-one-run-out cross-validation procedure was applied in which the classifier was trained on seven runs of data while tested on the remaining untrained run. The procedure was repeated for all runs ($k=8$). Due to excessive motion, only five runs of three participants were analyzed in the same manner for $k=5$ folds of cross-validation. A sphere of 3 mm radius searchlight was moved across the whole brain mask. A linear SVM was run as described above for each sphere, and the central voxel was assigned with a classification accuracy score. For each subject, the accuracy minus chance nifti files were created to be used for the group level analysis. One-sample t-test was applied with a threshold of $p < .05$, FWE-corrected. Each of six experimental conditions was labeled accordingly in each classification: HBM, HSCR, HNone, LBM, LSCR, LNone.

2.6.3 ROI Analyses

In order to examine the effect of AL on the core nodes of the BM processing network individually, ROI analyses were conducted. First of all, the ROIs were identified by subtracting the fixation blocks from all experimental block conditions. A total of three regions constituting BM processing network were created as 8-mm spheres for both hemispheres by using MarsBar [91]: (1) OTC in the left hemisphere centered at -45 -76 -2; (2) Parietal cortex in the left hemisphere centered at -30 -56 51; (3) PMC in the left hemisphere centered at -40 -3 49; (4) OTC in the right hemisphere centered at 30 -93 -5; (5) Parietal cortex in the right hemisphere centered at 37 -45 47; (6) PMC in the right hemisphere centered at 36 -3 53 (Figure 2.2).

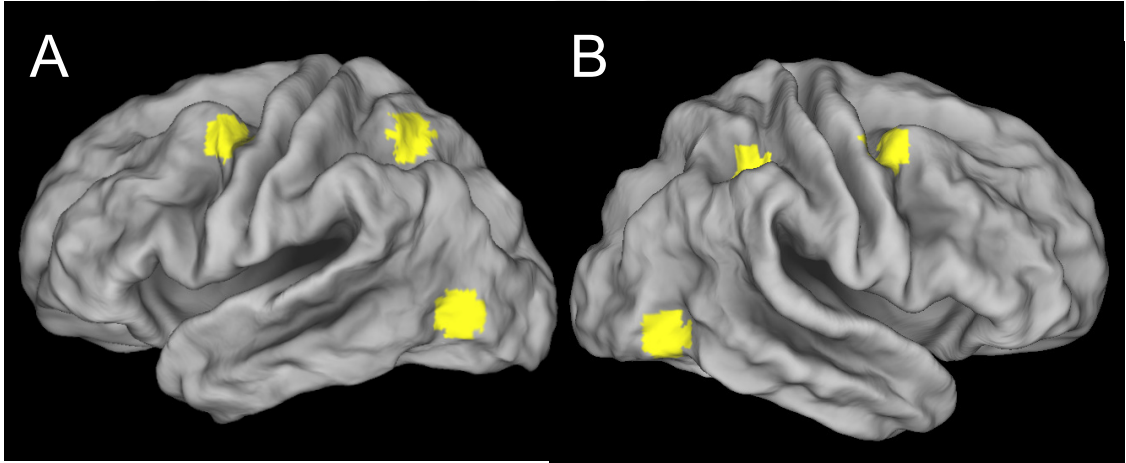


Figure 2.2: **ROI masks shown on the inflated brain.** Three spheres of 8-mm radius representing the OTC, Parietal, and PMC ROIs on left (A) and right (B) hemispheres.

2.6.3.1 ROI-Univariate Analysis

The group level flexible factorial analysis was run inclusively with the above-mentioned ROI masks. In order to examine the activity profiles across ROIs for the AL modulation on PS, mean beta values of BM minus None and SCR minus None contrasts in each AL condition were calculated. Then, a paired sample t-test was run with a threshold of $p < .05$, Bonferroni-corrected.

2.6.3.2 ROI-based MVPA

MVPA was run on individual ROIs using the same parameters as in searchlight whole-brain MVPA ($C=1$, 8-fold leave-one-run-out cross-validation, a sphere of 3 mm radius). The binary classifications were labeled accordingly and run as follows: (1) LBM versus LNone; (2) HBM versus HNone; (3) LSCR versus LNone; (4) HSCR versus HNone; (5) BM versus None; (6) SCR versus None; (7) Three-way classification of BM, SCR, and None. The accuracy minus chance brain images acquired from these classifications were then inputted to a one-sample t-test over all subjects for the group level analysis with a threshold of $p < .05$, FWE-corrected.

Chapter 3

Results

3.1 Behavioral Results

3.1.1 Accuracy

The overall accuracy of participants was over 80 percent. Thus, it can be said that the task was completed successfully by participants. There was a main effect of AL ($F(1,30) = 85.307, p < 0.001, \eta^2 = 0.671$) such that the accuracy rate in the low load ($M = 0.97, SD = 0.03$) was significantly higher than that of high load ($M = 0.84, SD = 0.081$). There was no main effect of PS ($F(1,30) = 1.231, p = 0.299$), and no interaction between the load and the PS conditions ($F(1,30) = 2.071, p = 0.135$). The results showed that regardless of the PS, the AL effect was evident on the accuracy rates.

3.1.2 Reaction Times

Reaction times (RT) analysis showed that there was a significant main effect of both AL ($F(1,30) = 82.507, p < 0.001, \eta^2 = 0.33$) and PS ($F(1,30) = 115.956, p < 0.001, \eta^2 = 0.273$). The RTs found in the high load was significantly higher

than that of low load ($t(30) = 8.897$, $p < 0.001$). Interestingly, post-hoc tests on the PS conditions showed that RTs in the None condition was significantly higher than that of BM ($t(30) = 12.976$, $p < 0.001$) and SCR ($t(30) = 13.391$, $p < 0.001$) conditions.

Moreover, a significant interaction between the load and PS was also found ($F(1,30) = 134.214$, $p < 0.001$, $\eta^2 = 0.168$). Post-hoc tests on each of six conditions revealed that although there was a significant difference between the HBM and HNone conditions ($t(30) = -18.497$, $p < 0.001$), SCR and BM conditions did not significantly differ from each other under the high load (HBM > HSCR: $t(30) = 0.993$, $p = 1$). Similarly, under high load, RTs in the SCR condition were statistically less than that of None condition ($t(30) = -19.490$, $p < 0.001$); yet, there was no difference between SCR and None conditions under low attentional load ($t(30) = -2.146$, $p = 0.512$). Overall, our results revealed that the attentional load effect was evident on each PS condition. Interestingly, participants responded faster when there was a task-irrelevant stimulus in the periphery; but there was no difference between the intact and scrambled BM conditions (Figure 3.1).

3.2 Whole-brain Analyses

In order to examine the whole-brain activity maps during the bottom-up perception of BM, we have conducted whole-brain within-subject flexible factorial (FF) and multivariate pattern analyses (MVPA). All results are thresholded at FWE-corrected, $p < 0.05$; and the peak-level results are reported.

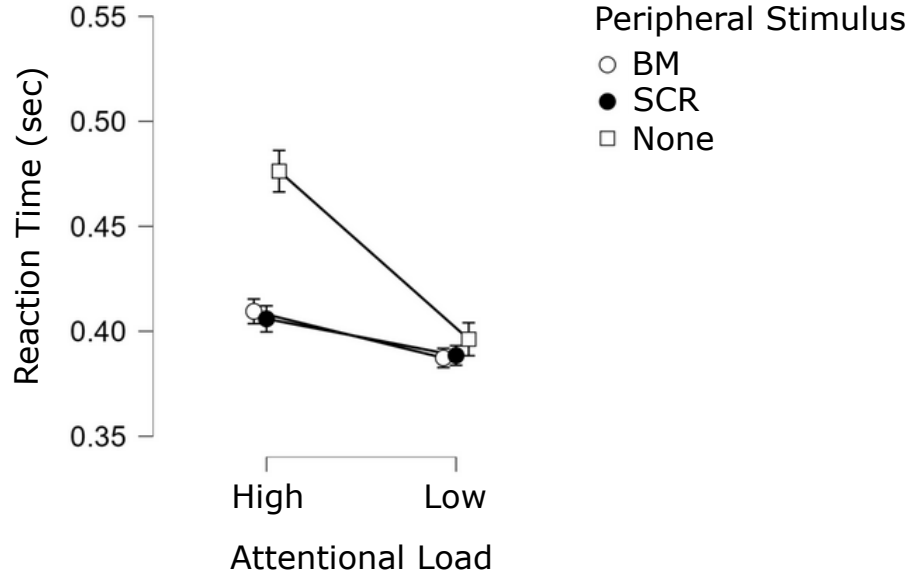


Figure 3.1: **Reaction times.** Reaction time values for experimental conditions are displayed. Error bars represent confidence interval (95%). P-value was adjusted for Bonferroni correction.

3.2.1 Univariate Results

3.2.1.1 Main effect of Attentional Load

Main effect of AL as indicated by an F-test on high and low AL blocks yielded two distinct network activity: Fronto-parietal attention network and default mode network (DMN) (Figure 3.2).

During High >Low contrast, significant activation ($p < 0.05$, FWE-corrected) was found within the left inferior parietal lobule (peak: -25 -70 42; $F = 104.65$) and left superior frontal gyrus (peak: -31 -4 69; $F = 86.81$) that constitute the fronto-parietal attention network (Figure 3.2). This finding is in line with the results of previous studies [62, 60, 63]. Additionally, bilateral posterior medial frontal gyrus that is associated with error-monitoring and signaling post-error adjustments [92] were found significantly activated ($p < 0.05$, FWE-corrected; peak= -4 9 53; $F = 81.87$) (peak= 27 -7 49; $F = 69.01$). In the Low >High t-contrast, DMN regions

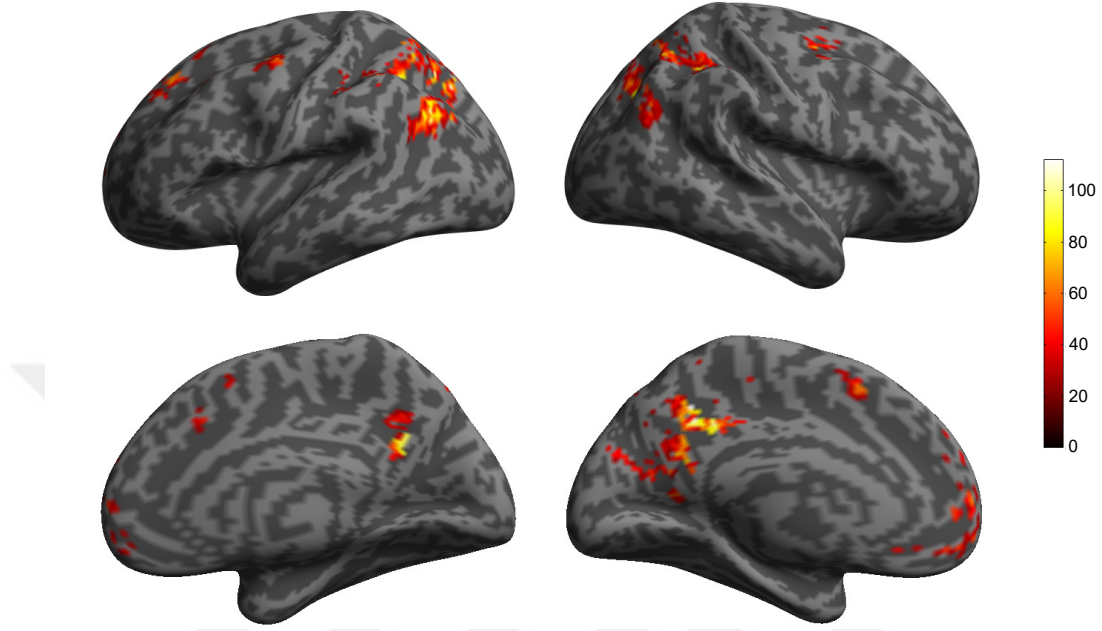


Figure 3.2: **The activity maps of the main effect of attentional load.** The F-test results showed fronto-parietal attention and DMN region activations. Results were FWE-corrected, at a threshold of $p < .05$.

[93] were observed. Activity maps included significant results ($p < 0.05$, FWE-corrected) in left precuneus (peak: -4 -55 19; $F = 127.55$), left and right angular gyri (peak: -46 -79 37; $F = 115.7$) (peak: 51 -73 34; $F = 74.16$), and left middle orbital gyrus (peak: -1 60 -11; $F = 108.52$) (Figure 3.2; Table 3.1).

3.2.1.2 Main effect of Peripheral Stimulus

In order to examine the recruited brain areas that are involved in bottom-up processing of BM stimuli, the main effect as well as pairwise t-contrasts of PS conditions were tested. The main effect of PS as indicated by an F-test on BM, SCR, and None conditions yielded significant bilateral activity maps ($p < 0.001$, uncorrected) in secondary visual (BA18) and visual association (BA19) cortices including motion sensitive MT/V5 region as expected (Figure 3.5): left and right lingual gyrus (peak: -19 -88 -11; $F = 32.3$), (peak: 21 -88 -9; $F = 29.44$); left and right middle occipital gyrus (peak: -46 -73 9; $F = 31.41$), (peak: 54 -76 2; $F = 27.38$); left superior occipital gyrus (peak: -10 -100 14; $F = 27.59$); and, left

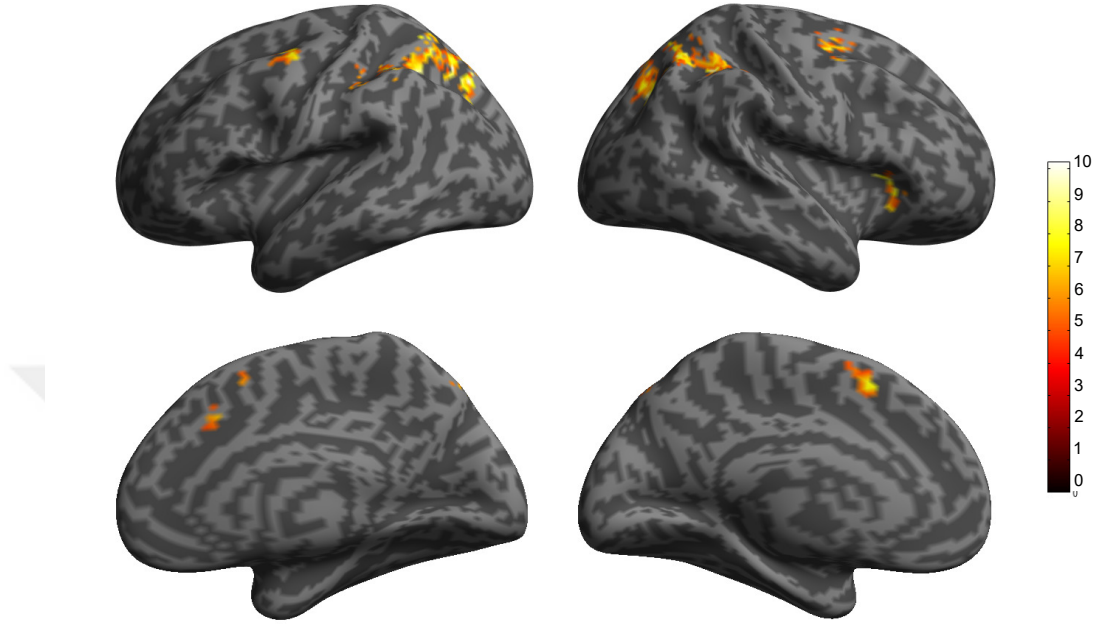


Figure 3.3: **The activity maps of the High >Low attentional load t-contrast.** The t-contrast of High >Low showed fronto-parietal network activation. Results were FWE-corrected, at a threshold of $p < .05$.

inferior occipital gyrus (peak: -31 -82 -11; $F = 25.88$).

Furthermore, separate comparisons between separate PS and None conditions yielded similar activities for both BM >None and SCR >None t-contrasts (Table 3.2). Accordingly, bilateral secondary visual (BA18) and visual association (BA19) cortices including motion-sensitive MT/V5 regions yielded significant activation ($p < 0.001$, uncorrected) (Figure 3.6 and Figure 3.7). Contrary to our expectation, there was no difference between intact and scrambled BM stimuli.

3.2.1.3 Attentional Load Modulation on Peripheral Stimulus

AL modulation on PS is indicated by the decreased or diminished activity maps in high load blocks as compared to low load blocks. Accordingly, while there was significant activation found within the OTC regions towards the BM >None and SCR >None contrasts under low load, only an early visual cortex region showed activity towards the same contrasts under high load. More specifically, we found

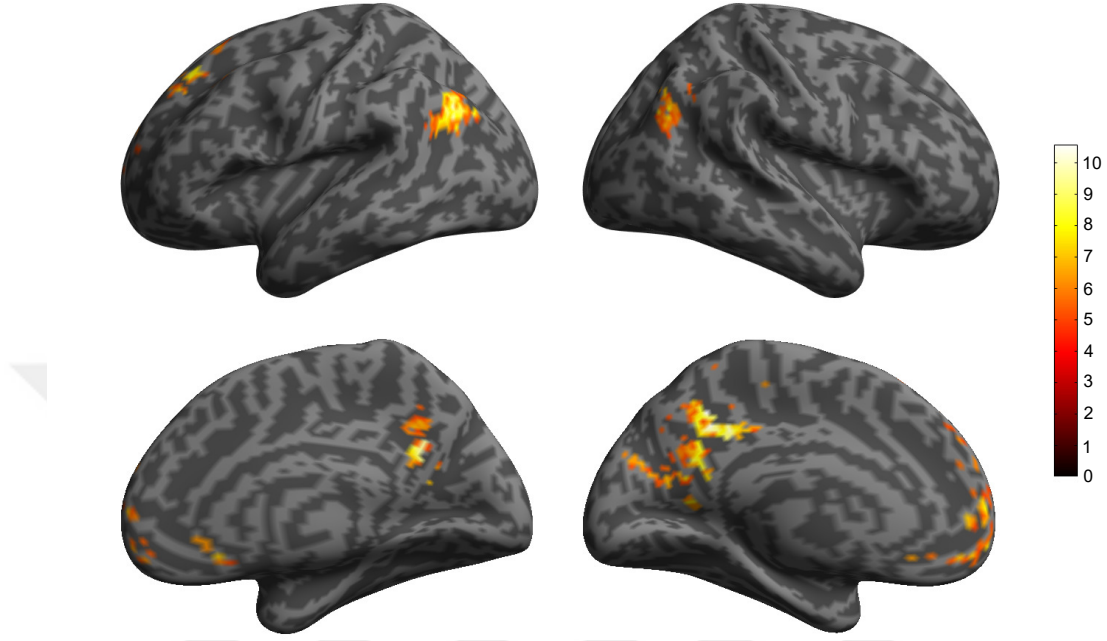


Figure 3.4: **The activity maps of the Low >High attentional load t-contrast.** The t-contrast of Low >High showed activation within DMN. Results were FWE-corrected, at a threshold of $p < .05$.

significant activation ($p < 0.001$, uncorrected) within bilateral middle occipital gyrus (Left: peak: -46 -73 9, $T = 7.14$; Right: peak: 54 -76 2, $T = 6.76$), lingual gyrus (peak: -19 -88 -11, $T = 6.34$) and inferior occipital gyrus (peak: -28 -85 -11, $T = 6.10$) in the left hemisphere for BM minus None contrast under low attentional load. As expected, there we found a decrease in the extent of activity maps for the same contrast under high AL and only lingual gyrus (peak: 15 -91 -14; $T = 5.24$) in the right hemisphere yielded significant activation ($p < 0.001$, uncorrected).

Results were similar for the SCR >None contrast. Under low load, there were significant activations ($p < 0.001$, uncorrected) within the OTC regions including: bilateral middle occipital gyrus (Left: peak: -52 -76 7, $T = 6.69$; Right: peak: 51 -73 2, $T = 6.08$), left inferior occipital gyrus (peak: -31 -82 -11; $T = 6.43$) left middle occipital gyrus (peak: -43 -82 2; $T = 5.65$), right fusiform gyrus (peak: 27 -79 -6; $T = 6.44$), and right lingual gyrus (peak: 21 -88 -9; $T = 6.26$). As expected, the activity maps found significant for the same contrast within high load included only the calcarine gyrus (peak: -4 -94 -6; $T = 5.42$) and lingual gyrus

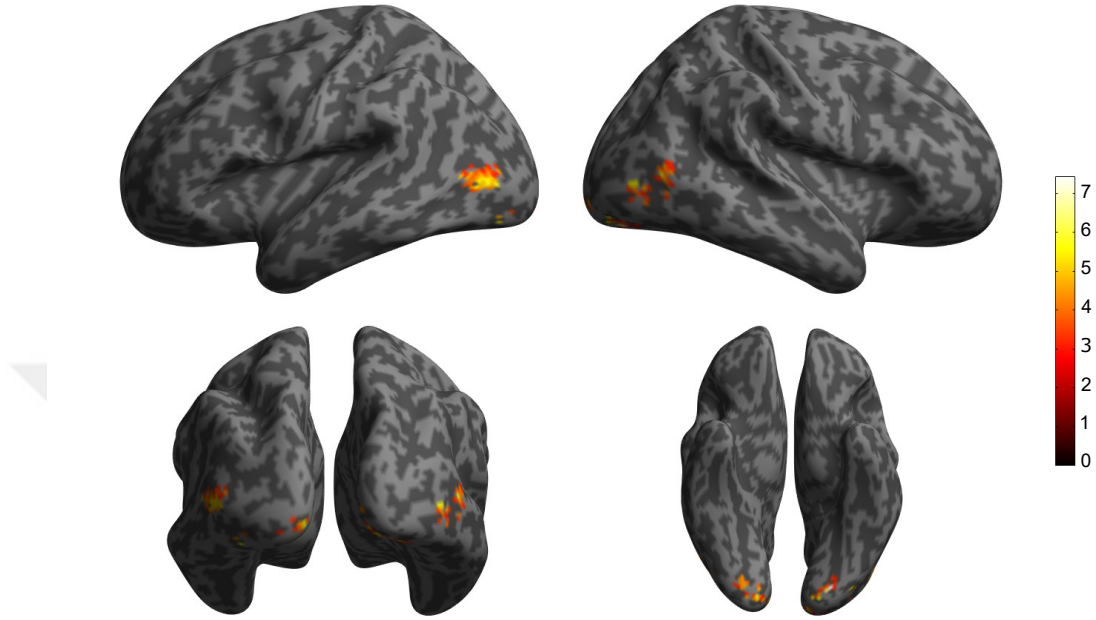


Figure 3.5: **The activity maps of the main effect of peripheral stimulus.** The F-test results showed activity maps in medial early visual cortex and motion-sensitive regions in the OTC. Results were at an uncorrected threshold of $p < .001$.

(peak: -19 -88 -11; $T = 5$) in the left hemisphere ($p < 0.001$, uncorrected)(Table 3.3).

3.2.2 Searchlight based MVPA

In order to test which brain regions could discriminate between each peripheral stimulus and None conditions, we ran MVPA. The group-level one sample t-test results on chance minus accuracy brain images of each participant was calculated on following binary classifications: BM vs None, LBM vs LNone, HBM vs HNone, SCR vs None, LSCR vs LNone, HSCR vs HNone.

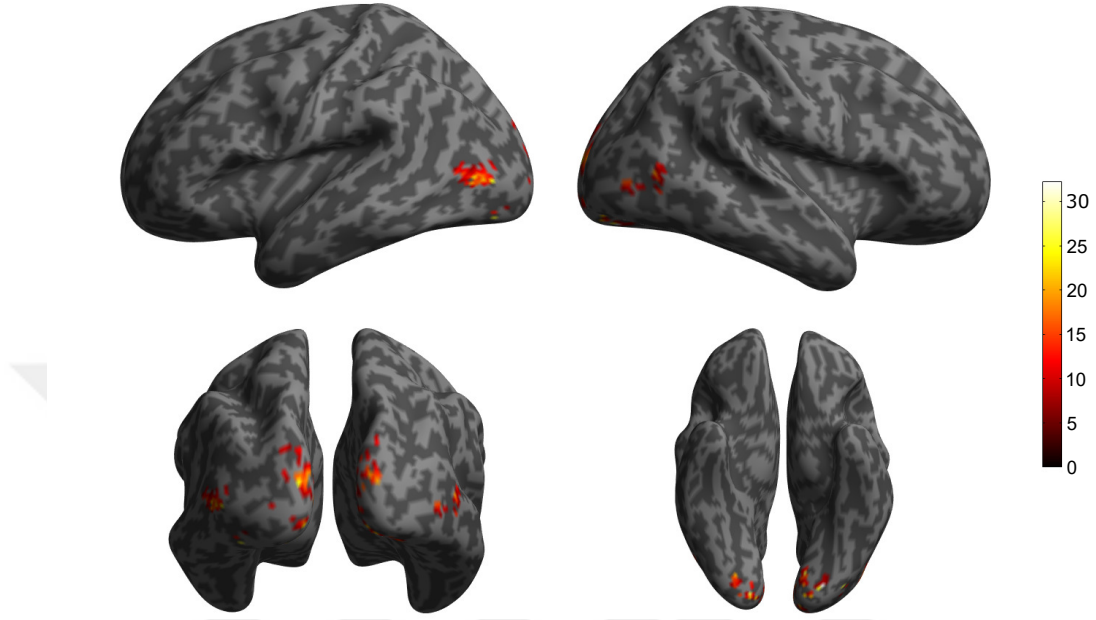


Figure 3.6: **The activity maps of the BM >None t-contrast.** The t-contrast of BM >None showed activation at motion-sensitive regions in the OTC. Results were at an uncorrected threshold of $p < .001$.

3.2.2.1 BM vs None Classification Results

Regardless of the attentional load block, motion and form sensitive regions in OTC could significantly decode BM and None conditions ($p < 0.05$, FWE-corrected)(Figure 3.8). The AL modulation was evident as indicated by the diminished extent and amount of the regions that could discriminate between the BM and None classes under the high load as compared to low load (Figure 3.9).

Specifically, the decoding regions for BM vs None were at peak in the bilateral middle occipital gyrus (Left: peak: -46 -82 4; $T = 9.92$; Right: peak: 42 -73 4; $T = 7$) and left lingual gyrus (peak: -16 -88 -14; $T = 15.4$) ($p < 0.05$, FWE-corrected). For the same comparison under low attentional load, the regions that could significantly ($p < 0.05$, FWE-corrected) separate LBM and LNone classes included calcarine gyrus (peak: -13 -97 -4; $T = 15.51$) and middle occipital gyrus (peak: -49 -79 2; $T = 10.5$) in the left hemisphere, in addition to the lingual gyrus (peak: 24 -85 -14; $T = 7.13$) in the right hemisphere. As expected, due to the modulation of attentional load, the same comparison under high load showed

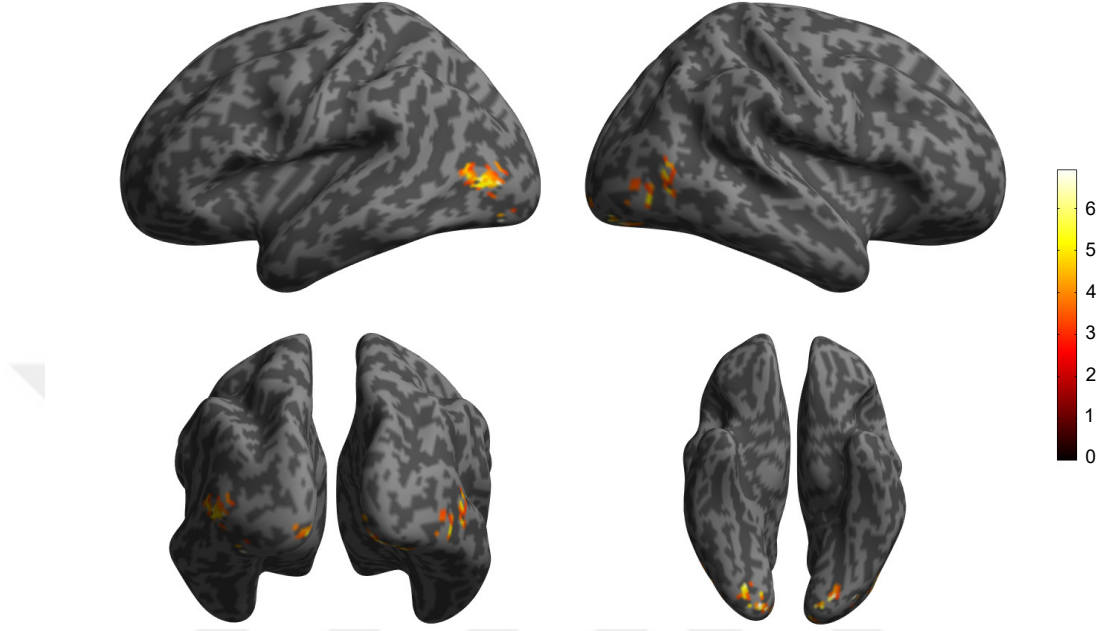


Figure 3.7: **The activity maps of the SCR >None t-contrast.** The t-contrast of SCR >None yielded activation at motion-sensitive regions in the OTC. Results were at an uncorrected threshold of $p < .001$.

only calcarine gyrus in the left hemisphere (peak: -10 -91 -4; $T = 13.59$) as the region that significantly separates HBM and HNone from each other ($p < 0.05$, FWE-corrected) (Table 3.4).

3.2.2.2 SCR vs None Classification Results

The SVM could discriminate between the SCR and None conditions over all AL blocks at the motion and form sensitive OTC regions ($p < 0.05$, FWE-corrected)(Figure 3.10). The modulation of AL was evident as indicated by the decreased amount and extension of decoding regions in the high load as compared to that of low load (Figure 3.11).

Specifically, regardless of the AL block, SCR versus None classification could be significant decoded at fusiform gyrus (peak: -22 -82 -11; $T = 14.32$) and middle occipital gyrus (peak: -49 -76 14; $T = 9.38$; peak: -31 -70 -6; $T = 6.79$) in the left hemisphere ($p < 0.05$, FWE-corrected). Moreover, under the low load, SCR and

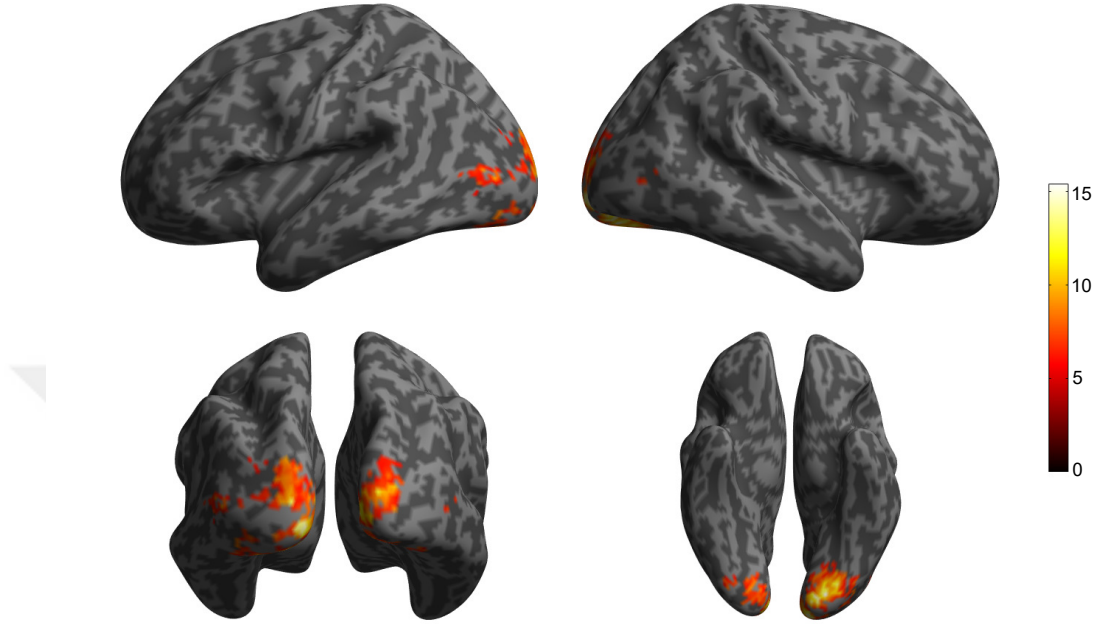


Figure 3.8: **Decoding regions of the BM versus None classification.** Motion and form sensitive OTC regions were shown to discriminate BM and None conditions regardless of the attentional load. Results were FWE-corrected, at a threshold of $p < .05$.

None conditions could be discriminated significantly at the calcarine gyrus (peak: -10 -94 -4; $T = 12.13$), superior occipital gyrus (peak: -19 -97 17; $T = 9.06$), and middle occipital gyrus (peak: -52 -82 4, $T = 7.12$) regions in the left hemisphere ($p < 0.05$, FWE-corrected). Under high load, the same comparison of SCR and None conditions yielded peak coordinates at calcarine (peak: -7 -91 -6, $T = 14.85$) and superior occipital gyrus (peak: -13 -97 19, $T = 9.28$) regions in the left hemisphere ($p < 0.05$, FWE-corrected)(Table 3.4).

3.3 ROI Analyses

Based on the contrast of all experimental blocks minus fixation, we have created three ROIs for each hemisphere that constitute the BM processing network: OTC, parietal cortex, and PMC.

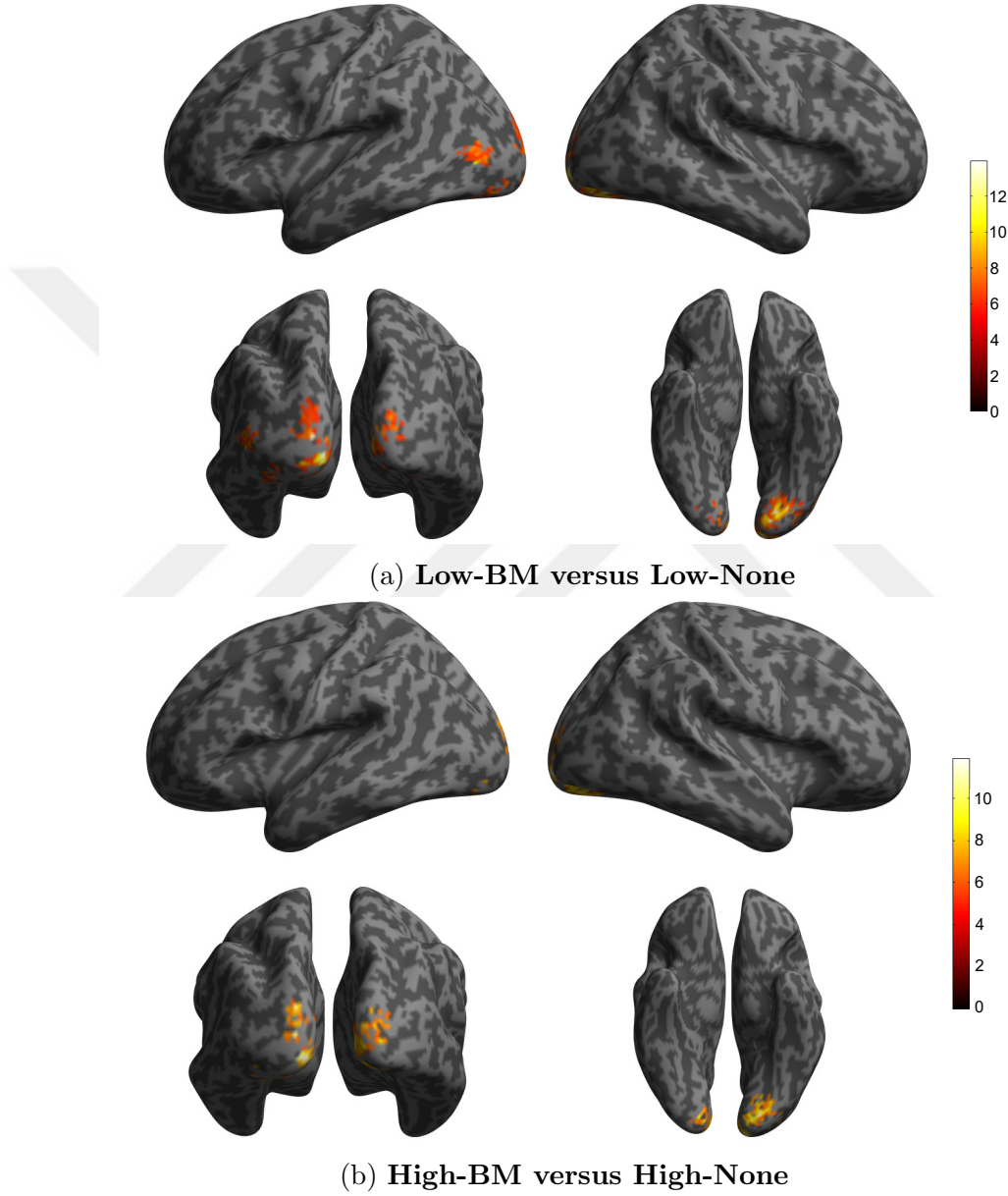


Figure 3.9: **Attentional load modulation on BM.** Attentional load modulation on BM was evident. (a) Under low attentional load, BM and None could be decoded in the OTC regions; while (b) under high load, only the early visual areas could discriminate BM and None stimuli. Results were FWE-corrected, at a threshold of $p < .05$.

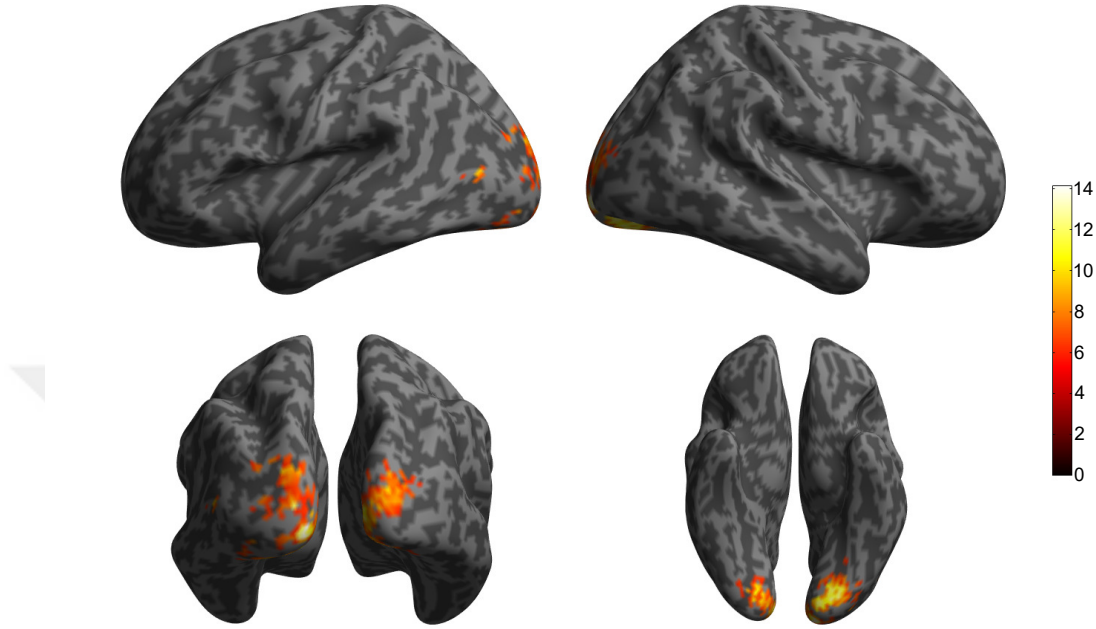


Figure 3.10: **Decoding regions of the SCR versus None classification.** Motion sensitive regions in OTC could discriminate SCR and None conditions regardless of the attentional load. Results were FWE-corrected, at a threshold of $p < .05$.

3.3.1 Univariate ROI Results

In order to test how each BM processing region responds to the task-irrelevant peripheral stimulus conditions, univariate ROI analysis was run on bilateral OTC, Parietal, and PMC regions. In line with the whole-brain group analysis results, for both hemispheres and for both intact and scrambled BM stimuli, the activation was constrained to the OTC (Table 3.5). The results indicated a significant peak activity for BM >None contrast as well as the LBM >LNone contrast at the OTC region in the left hemisphere (peak: -43 -82 2, $T = 5.81$; peak: -43 -82 2, $T = 6.2$) ($p < 0.05$, FWE-corrected). Similarly, for the contrasts of SCR >None and LSCR >LNone, a significant peak activity was observed within the left OTC (peak: -43 -82 2, $T = 6.43$; peak: -43 -82 2, $T = 5.65$) ($p < 0.05$, FWE-corrected). There was no significant activation within the OTC towards the HBM >HNone and HSCR >HNone contrasts. This lack of activity at the occipito-temporal ROI for the high load contrasts is an indicator of the AL modulation on both intact and scrambled BM stimuli. Moreover, parietal and PMC regions were not activated

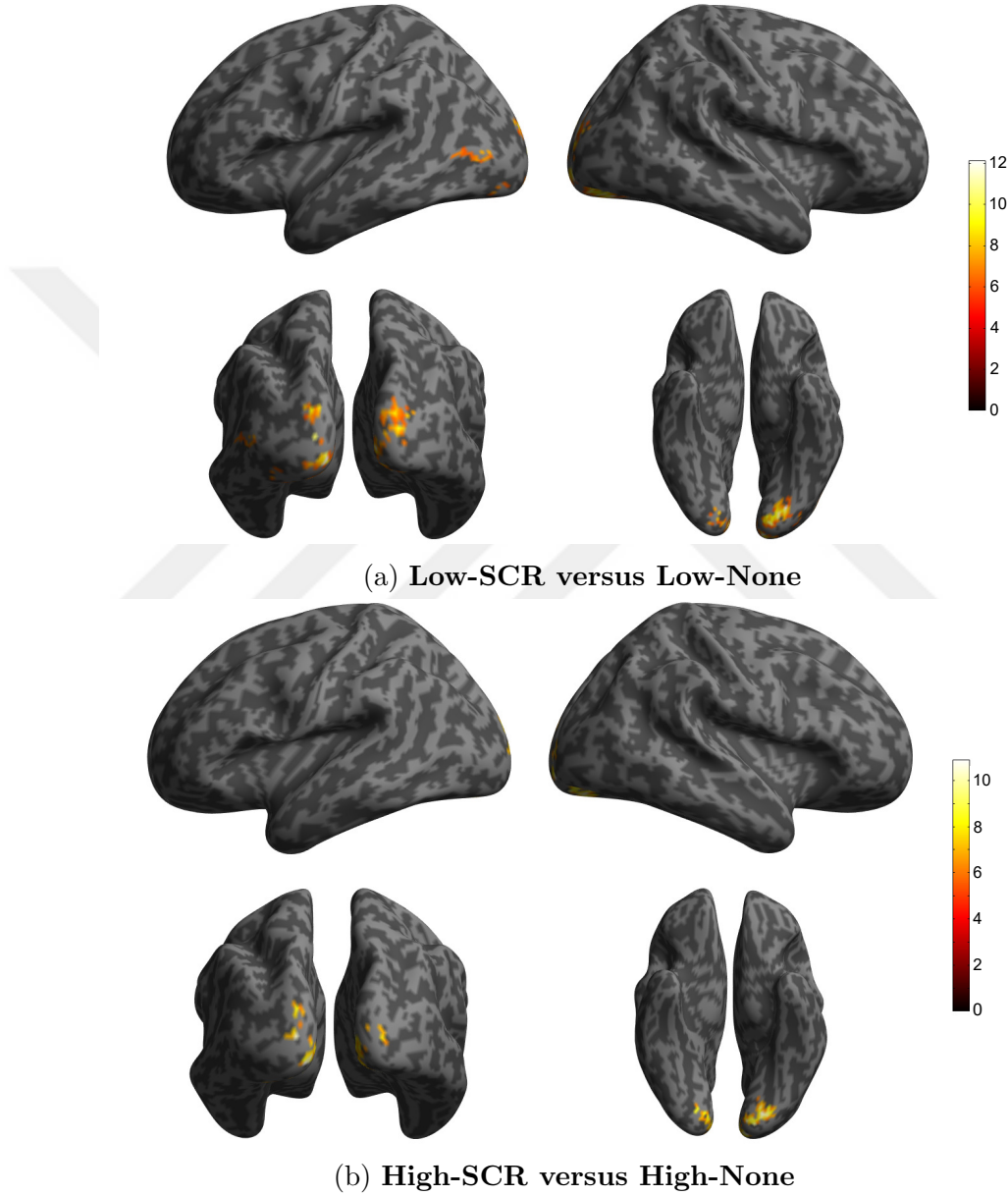


Figure 3.11: **Attentional load modulation on SCR.** Attentional load modulation on SCR was evident. (a) Under low attentional load, SCR and None could be decoded in the motion sensitive OTC regions; while (b) under high load, only the early visual areas could discriminate SCR and None stimuli. Results were FWE-corrected, at a threshold of $p < .05$.

in any of the contrasts.

In order to study the AL modulation on BM quantitatively, each participants' mean beta values for LBM >LNone and HBM >HNone, as well as LSCR >LNone and HSCR >HNone contrasts were tested as a paired-samples t-test in all ROIs (Figure 3.12). Results indicated that for the intact BM stimuli, there was a significant AL modulation at bilateral occipito-temporal (Left: $t(30)= 5.601$, $p <.001$; Right: $t(30)= 4.832$, $p <.001$) and right parietal cortex ($t(30)= 3.51$, $p <.001$) as indicated by the mean beta value difference between low and high attentional load. There was no difference between these conditions within the left parietal cortex ($t(30)= 2.33$, $p = 0.027$) and any side of the PMC (Left: $t(30)= 1.106$, $p = 0.278$; Right: $t(30)= 2.056$, $p = 0.049$). For the effect of attentional load on the processing of scrambled BM stimuli, we have compared L-SCR >LNone contrast with H-SCR >HNone across each ROI in both hemispheres. The effect of AL as indicated by decrease in beta values in high load as compared to that of low load blocks was significant only at bilateral occipito-temporal ROIs (Left: $t(30)= 3.805$, $p <.001$; Right: $t(30)= 4.102$, $p <.001$). Unlike intact BM, the effect of AL was not present in the parietal cortex for the scrambled BM stimuli (Left: $t(30)= 2.007$, $p= 0.054$; Right: $t(30)= 1.589$, $p= 0.123$); and similarly no significant difference in mean beta values was observed in PMC (Left: $t(30)= 1.668$, $p= 0.106$; Right: $t(30)= 1.761$, $p= 0.316$).

3.3.2 Multivariate ROI Results

The ROI-based MVPA results differed from the univariate ROI analysis. Unlike the univariate ROI analysis, decoding results for BM vs None and LBM vs LNone classifications were significant within the bilateral OTC regions (BM vs None: Left: peak: -49 -79 -9, $T= 5.13$; Right: peak: 45 -73 -11, $T= 4.17$; LBM vs LNone: Left: peak: -49 -79 9, $T= 7.13$; Right: peak: 45 -73 -11, $T= 5.44$; $p <0.05$, FWE-corrected). Interestingly, while decoding results for the LSCR vs LNone classification was significant in bilateral OTC (Left: peak: -49 -79 -9, $T= 5.32$; Right: peak: 45 -73 -11, $T= 4.56$; $p <0.05$, FWE-corrected); for the SCR

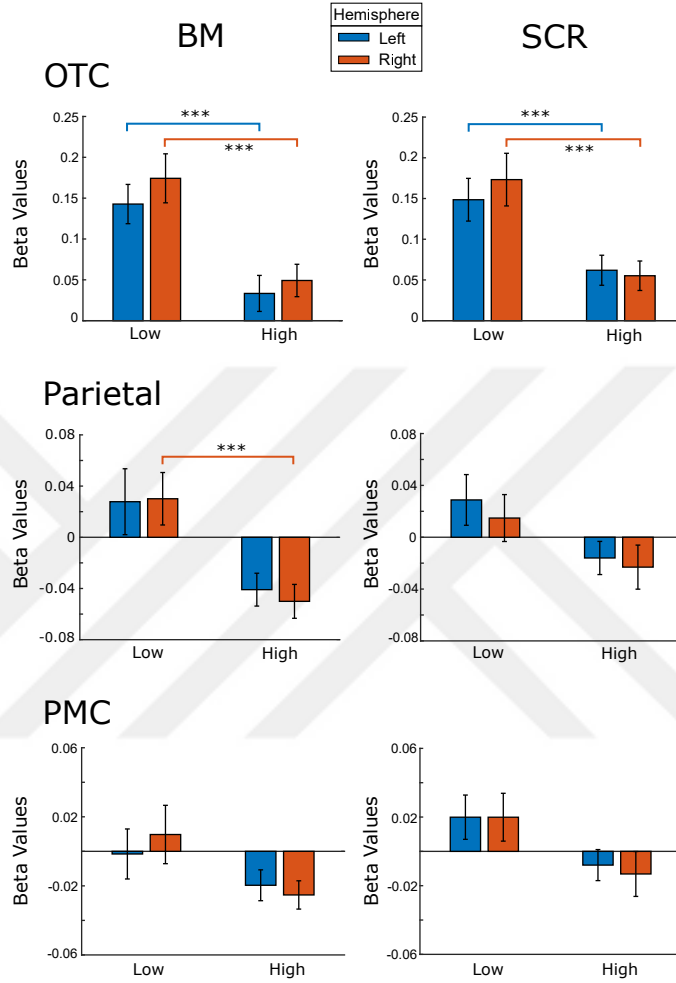


Figure 3.12: **Beta values across BM and SCR >None conditions.** Attentional load modulation indicated by a significant decrease in the beta values of both BM and SCR >None under high load compared to low load. Results were at a threshold of $p < .05$, Bonferroni-corrected.

vs None classification, only the left OTC were significant (peak: -49 -79 -9, $T = 3.98$; $p < 0.05$, FWE-corrected) as in the univariate ROI results. Decoding results for the HSCR vs HNone and HBM vs HNone classifications were not significant in any of the regions (Table 3.6).

Table 3.1: **Main effect of attentional load.** Results were FWE-corrected, at a threshold of $p < .05$.

Main effect of attentional load		
<i>Region</i>	<i>Coordinates</i>	<i>F-Score</i>
L Precuneus	-4 -55 19	127.55
L Angular Gyrus (BA23)	-46 -79 37	115.7
L Middle Orbital Gyrus (BA39)	-1 60 -11	108.52
L Inferior Parietal Lobule (BA39)	-25 -70 42	104.65
L Superior Frontal Gyrus (BA6)	-31 -4 69	86.81
L Posterior-Medial Frontal (BA6)	-4 9 52	81.87
R Middle Occipital Gyrus (BA7)	30 -67 32	85.15
R Angular Gyrus (IPL) (BA39)	51 -73 34	74.16
R Middle Frontal Gyrus (BA6)	27 -7 49	69.01
High >Low		
<i>Region</i>	<i>Coordinates</i>	<i>F-Score</i>
L Inferior Parietal Lobule (BA39)	-25 -70 42	10.23
L Superior Frontal Gyrus (BA6)	-31 -4 69	9.32
L Posterior-Medial Frontal (BA6)	-4 9 52	9.05
R Middle Occipital Gyrus (BA7)	30 -67 24	9.23
R Insula Lobe (BA45)	33 24 9	8.65
R Middle Frontal Gyrus (BA6)	27 -7 49	8.31
Low >High		
<i>Region</i>	<i>Coordinates</i>	<i>F-Score</i>
L Precuneus (BA23)	-4 -55 19	11.29
L Angular Gyrus (BA39)	-46 -79 37	10.76
L Middle Orbital Gyrus (BA10)	-1 60 -11	10.42
R Angular Gyrus (BA39)	51 -73 34	8.61

Table 3.2: **Main effect of peripheral stimulus.** Results were at an uncorrected threshold of $p < .001$.

Main effect of peripheral stimulus		
<i>Region</i>	<i>Coordinates</i>	<i>F-Score</i>
L Lingual Gyrus (BA18)	-19 -88 -11	32.3
L Middle Occipital Gyrus (BA19)	-46 -73 9	31.41
L Superior Occipital Gyrus (BA18)	-10 -100 14	27.59
L Inferior Occipital Gyrus (BA18)	-31 -82 -11	25.88
R Lingual Gyrus (BA18)	21 -88 -9	29.44
R Middle Occipital Gyrus (BA19)	54 -76 2	27.38
BM >None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Lingual Gyrus (BA18)	-19 -88 -11	7.44
L Middle Occipital Gyrus (BA19)	-52 -82 7	7.41
L Inferior Occipital Gyrus (BA18)	-28 -85 -11	6.26
R Middle Occipital Gyrus (BA19)	54 -76 2	7.01
R Lingual Gyrus (BA18)	15 -91 -14	6.85
SCR >None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Inferior Occipital Gyrus (BA18)	-31 -82 -11	6.79
L Middle Occipital Gyrus (BA19)	-46 -73 9	6.55
L Lingual Gyrus (BA18)	-19 -88 -11	6.53
R Lingual Gyrus (BA18)	21 -88 -9	7.17
R Fusiform Gyrus (BA18)	27 -79 -6	6.17
R Middle Occipital Gyrus (BA19)	54 -76 2	5.73
BM >SCR		
<i>No activity</i>		

Table 3.3: **Attentional load modulation on peripheral stimulus.** Results were at an uncorrected threshold of $p < .001$.

Low-BM >Low-None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Middle Occipital Gyrus (BA19)	-46 -73 9	7.14
L Lingual Gyrus (BA18)	-19 -88 -11	6.34
L Inferior Occipital Gyrus (BA18)	-28 -85 -11	6.1
R Middle Occipital Gyrus (BA19)	54 -76 2	6.76
High-BM >High-None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
R Lingual Gyrus (BA18)	15 -91 -14	5.24
Low-SCR >Low-None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Middle Occipital Gyrus (BA19)	-52 -76 7	6.69
L Inferior Occipital Gyrus (BA18)	-31 -82 -11	6.43
L Middle Occipital Gyrus (BA19)	-43 -82 2	5.65
R Fusiform Gyrus (BA18)	27 -79 -6	6.44
R Lingual Gyrus (BA18)	21 -88 -9	6.26
R Middle Temporal Gyrus (BA37)	51 -73 2	6.08
High-SCR >High-None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Calcarine Gyrus (BA18)	-4 -94 -6	5.42
L Lingual Gyrus (BA18)	-19 -88 -11	5

Table 3.4: **Attentional load modulation on BM indicated by the diminished extent of decoding regions.** Results were FWE-corrected, at a threshold of $p < .05$.

BM vs None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Lingual Gyrus (BA18)	-16 -88 -14	15.4
L Middle Occipital Gyrus (BA19)	-46 -82 4	9.92
R Middle Occipital Gyrus (BA19)	42 -73 4	7
Low-BM vs Low-None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Calcarine Gyrus (BA18)	-13 -97 -4	15.51
L Middle Occipital Gyrus (BA19)	-49 -79 2	10.5
R Lingual Gyrus (BA18)	24 -85 -14	7.13
High-BM vs High-None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Calcarine Gyrus (BA18)	-10 -91 -4	13.59
SCR vs None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Fusiform Gyrus (BA18)	-22 -82 -11	14.32
L Middle Occipital Gyrus (BA19)	-46 -76 14	9.38
L Middle Occipital Gyrus (BA19)	-31 -70 -6	6.79
Low-SCR vs Low-None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Calcarine Gyrus (BA18)	-10 -94 -4	12.13
L Superior Occipital Gyrus (BA18)	-19 -97 17	9.06
L Middle Occipital Gyrus (BA19)	-52 -82 4	8.67
High-SCR vs High-None		
<i>Region</i>	<i>Coordinates</i>	<i>T-Score</i>
L Calcarine Gyrus (BA18)	-7 -91 -6	14.85
L Superior Occipital Gyrus (BA18)	-13 -97 19	9.28

Table 3.5: **Univariate Distractor Contrasts within inclusive ROI masks.** Results were FWE-corrected, at a threshold of $p < .05$.

	BM >None		LBM >LNone		HBM >HNone	
	<i>Coordinates</i>	<i>T-Score</i>	<i>Coordinates</i>	<i>T-Score</i>	<i>Coordinates</i>	<i>T-Score</i>
LH-OTC	-43 -82 2	5.82	-43 -82 2	6.2	No activity	
RH-OTC	No activity		No activity		No activity	
	SCR >None		LSCR >LNone		HSCR >HNone	
	<i>Coordinates</i>	<i>T-Score</i>	<i>Coordinates</i>	<i>T-Score</i>	<i>Coordinates</i>	<i>T-Score</i>
LH-OTC	-43 -82 2	6.43	-43 -82 2	5.65	No activity	
RH-OTC	No activity		No activity		No activity	

Table 3.6: **MVPA Distractor Comparisons within inclusive ROI masks.**
Results were FWE-corrected, at a threshold of $p < .05$.

	BM vs None		LBM vs LNone		HBM vs HNone	
	<i>Coordinates</i>	<i>T-Score</i>	<i>Coordinates</i>	<i>T-Score</i>	<i>Coordinates</i>	<i>T-Score</i>
LH-OTC	-49 -79 -9	5.13	-49 -79 -9	7.13	No activity	
RH-OTC	45 -73 -11	4.17	45 -73 -11	5.44	No activity	
	SCR vs None		LSCR vs LNone		HSCR vs HNone	
	<i>Coordinates</i>	<i>T-Score</i>	<i>Coordinates</i>	<i>T-Score</i>	<i>Coordinates</i>	<i>T-Score</i>
LH-OTC	-49 -79 -9	3.98	-49 -79 -9	5.32	No activity	
RH-OTC	No activity		45 -73 -11	4.56	No activity	

Chapter 4

Discussion

In the current study, we have examined whether such an ecologically and socially important stimulus as biological motion (BM) would be processed when it is not at the focus of attention; and if so, whether this processing would be modulated by the attentional load.

We hypothesized that BM would be processed in a bottom-up manner across regions of the BM processing network; and that it would be modulated by attentional load. In line with the previous literature, our results supported the incidental bottom-up processing of BM [1]. Furthermore, we found that the task-irrelevant peripheral BM stimulus was processed within the motion-sensitive OTC region. Lastly, we found that bottom-up processing of BM was modulated by attentional load. Our study is the first to examine the relationship between bottom-up and top-down processing of BM through an attentional load paradigm.

In this chapter, I will discuss our main findings as well as the limitations and future directions of our study.

4.1 The Bottom-up Perception of BM: Recruited Regions

The literature on neural processing of BM shows three core brain areas [9]: (1) The OTC including form and motion sensitive regions (i.e. EBA, FBA, hMT+) and STS as the integration hub as well as the meaning and action understanding related (2) parietal and (3) PMC regions (i.e. IPS, IPL, IFG, PMC). These regions support the BM perception under selective attention [2]. However, there are inconsistent results in terms of the regions that are associated with the bottom-up perception of BM [4, 15, 2]

In the current study, we found that regardless of the attentional load, OTC regions including motion sensitive areas were activated. These regions were evident specifically under low attentional load. However, under high attentional load, the activation was constrained to the early visual cortex regions. One can make two important inferences based on these findings: (1) In line with the previous literature on incidental processing of BM stimuli, visual feature encoding areas in the OTC were associated with the bottom-up processing of BM; (2) In addition to the role of OTC in incidental processing, the activation within the OTC was found to be modulated by a top-down factor that is attentional load. Thus, our results suggest that both bottom-up and top-down processing of BM is evident in the OTC. By being the first study to highlight this interaction, this finding emphasizes the need for studying bottom-up and top-down processes together.

There were two surprising findings in our results that we did not expect. Firstly, in terms of the recruited brain regions, there was no significant activation found in the STS. In the literature, there are inconsistent results towards the neural correlates of bottom-up BM perception. Some studies found activation only in EBA and hMT+ [4, 15], while some found additional activity in STS and IPS [2]. This disparity between results led us to exploratively hypothesize that under low attentional load, we could see activity maps in not only OTC, but also in STS and parietal cortex. However, our results were constrained to the OTC regions. This finding could be due to the main methodological difference

between our study and the study that found STS and IPS activity: The stimulus set. In Saygin and Sereno’s retinotopy study [2], participants’ field of view was populated by intact and scrambled BM stimuli. Meanwhile, in our study and studies of those that did not find STS activity [4, 15], only one BM stimulus was shown. Thus, the increased number of stimuli, as well as the contrasting nature of intact and scrambled PLDs might have resulted in stronger stimulation in the BM processing brain regions. Therefore, the possible reason why we did not see STS activity in our study could be that using one PLD of BM stimulus may not be strong enough to yield activation beyond visual feature encoding areas in the OTC.

The second surprising finding was that we did not find a significant difference between the intact and scrambled BM stimuli. Based on the literature showing stronger activation within the OTC and STS towards the intact compared to scrambled BM stimulus, we hypothesized that we would find distinct activity maps and stronger activation towards the intact PLDs of BM. However, our results did not yield any difference between scrambled and intact BM stimuli even under low attentional load. This finding may be due to the unsuccessful forming of BM representation indicated by the lack of STS activation. The previous literature showed that abstract action representation based on BM stimulus is formed in the STS. Moreover, Grossman and colleagues [23] have found that STS activation directly depended on participants’ ability to recognize PLDs as BM. In their perceptual learning study, only when participants could recognize the PLDs of BM stimulus under the noise mask, the STS activation was observed. Thus, it could be that our participants could not recognize the PLDs as BM and in turn we neither found difference between intact and scrambled BM stimuli, nor any significant STS activation. However, considering the successful completion of participants on a small task conducted prior to the MR scan in which participants indicated where the intact, not the scrambled, BM was shown on the laptop screen; this conclusion may be unlikely. It would be interesting to replicate our study with a similar stimulus set of Saygin and Sereno [2] and compare whether STS activity and difference between intact and scrambled BM would be observed.

4.2 Engagement of Top-down and Bottom-up Attention Networks

In addition to the bottom-up processing of BM as indicated by the main effect of peripheral stimuli, we have also found a main effect of attentional load evident in distinct network regions. In this study, participants had to direct their attention towards a main visual detection task that was shown at the fovea, while ignoring the task-irrelevant peripheral stimulus. Although the display of the foveal task was kept the same across experimental blocks, the attentional load of the main task was manipulated via increasing the demand of attention resources towards the main task. For the high load task, participants had to detect a conjunction of orientation and color (i.e. upright yellow and upside green t-shapes) rather than a pop-out feature of the t-shape (i.e. color: red shapes). Detecting the conjunction targets rather than the pop-out singleton required participants to focus on the foveal task more than the other [62]. Accordingly, the high load task demanded more attention as compared to low load task. Thus, in line with the previous literature [62, 60], during the High >Low load contrast as well as the High versus Low load classification (Appendix, Supplementary Figure A.1), we found the fronto-parietal network (FPN) regions indicating increased demand of attentional engagement towards the high load task.

Interestingly, in the Low >High attentional load contrast, we found activation in the default-mode network (DMN) regions. This is the very first evidence to see the interaction between DMN and FPN in an attentional load paradigm. In the working memory literature, it has been shown repeatedly that the DMN activity follows two distinct mechanisms. Firstly, it gets activated during the baseline state in which the participant is not involved in any cognitive task or is engaged in mind-wandering. Secondly, it deactivates during cognitively or attentionally demanding tasks that we see often in the working-memory literature such as performing arithmetics, recalling a set of strings or numbers, or similar to our study, giving response towards a predetermined target [94, 95, 96].

When we analyzed the DMN and FPN regions' activation in High >Low and

Low >High contrasts, we found that for the High >Low contrast, there is a significant activation in FPN with a deactivation in DMN regions; and the opposite is correct for the Low >High contrast (Appendix, Supplementary Figure B.1). This finding is in line with the triple network model that was proposed by Menon [97], in which as the FPN gets activated DMN regions show deactivation; and vice versa [98]. Although it was not the aim of this current study to examine the attention networks in depth, one might have expected to see the ventral attention network (VAN, saliency network) rather than the DMN. VAN is the third network in this triple model which is associated with the stimulus-driven processing of the unexpected, task-irrelevant stimuli [97]. The possible reason why we did not observe VAN activity during peripheral stimuli conditions could be that the biological motion stimulus shown at the periphery was not an unexpected event [99]. The amount of trials and the repetition of peripheral stimulus blocks were equal to each other. Also, before the study started, participants were familiarized with the BM stimuli and they were explicitly told that they may see to-be-ignored intact or scrambled BM stimuli at the periphery.

In sum, this is the very first study in the field of attentional load that shows the interplay between DMN and FPN regions. It was possible for us to find such a relationship, since in addition to the no-peripheral stimulus baseline condition, we also used a control stimulus (i.e. scrambled motion). This has led us to discriminate the attentional load modulation on the BM stimulus from the distinct brain regions that are associated with low and high attentional load tasks while being able to compare them separately.

4.3 Limitation

In the literature, attentional load is evident as diminished activation related with the task-irrelevant peripheral stimulus. One may suggest that the relatively stronger and extensive activation observed in the low load blocks may be due to the unintentional shift in the eye gaze towards the peripheral stimulus. This possibility could be relevant for our study as well. Considering the early preference

and recognition ability of humans towards BM stimuli, one may argue that participants might have shifted their eye gaze towards the peripheral BM stimulus unintentionally. Such shifts in the eye-gaze would yield activity maps similar to the perception of BM under selective attention. However, we did not find any region beyond OTC that could explain the involuntary eye-gaze towards the BM stimulus. So, although we did not use eye-tracker to check whether participants' eye gaze shifted away from the fixation task, our results show no sign of active viewing of peripheral BM stimuli even under low attentional load.

4.4 Future Directions

Our study shows that the bottom-up processing of BM is supported by motion and form sensitive regions in the OTC. This finding is in line with the model of Giese and Poggio [17]. Accordingly, in their model, there are two separate but parallel processes representing the form and motion pathways. Each pathway consists of an increasing hierarchy of neural feature detectors with increasing receptive field sizes and complexity. The significance of this model is that it clearly supports the immediate recognition, in other words, incidental processing of BM stimuli through feedforward processing. So, observing only the form and motion sensitive areas in the OTC during the bottom-up perception of BM in our study is in line with the model of Giese and Poggio [17]. However, our findings further showed that the OTC regions were modulated by attentional load. This top-down effect of attention on the same brain areas that showed bottom-up processing highlights the possibility of feedback projections. Thus, our findings emphasize the need for more comprehensive models that integrate these two processes and reflect their effect on the overall BM perception. Future studies may look further into building and testing such integrative models.

4.5 Conclusion

In this study we examined the bottom-up perception of BM under attentional load. We have found that even though the selective attention was directed at an attentionally demanding main task at the fovea, the peripheral task-irrelevant BM stimuli were processed incidentally. The neural correlates of this processing yielded activity in motion sensitive regions in the OTC. Therefore, our results show that the bottom-up perception of BM is supported by the visual feature encoding areas rather than higher level action understanding network regions.

Finally, the bottom-up processing regions observed in this study were also modulated by attentional load. Thus, our findings add onto the stimulus-driven processing models and studies of BM by showing direct evidence that the top-down and bottom-up perception of BM is interrelated.

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Appendix A

High versus Low Attentional Load Decoding Results

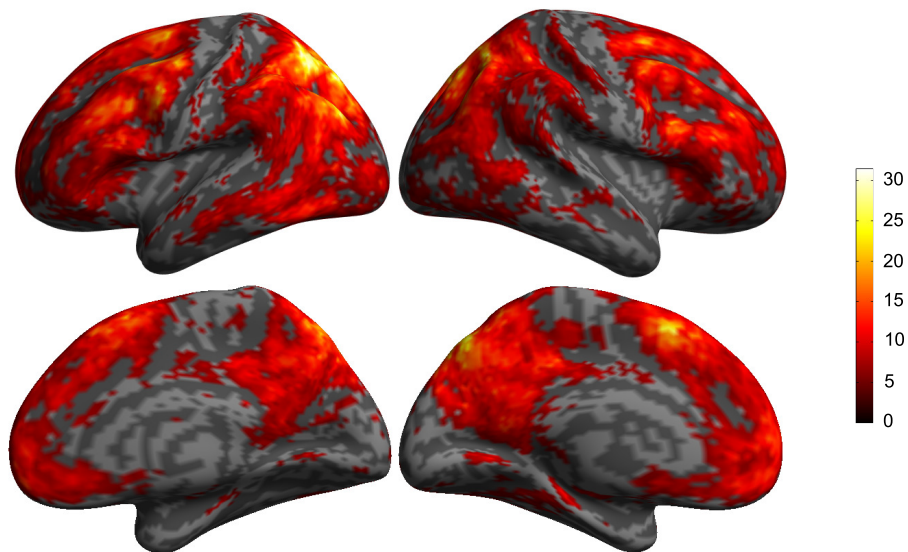


Figure A.1: **High versus Low Attentional Load Decoding Results.** MVPA results on high versus low load classification yielded significant decoding results in fronto-parietal network regions.

Appendix B

DMN and FPN Regions under
Low > High and High > Low
Contrasts

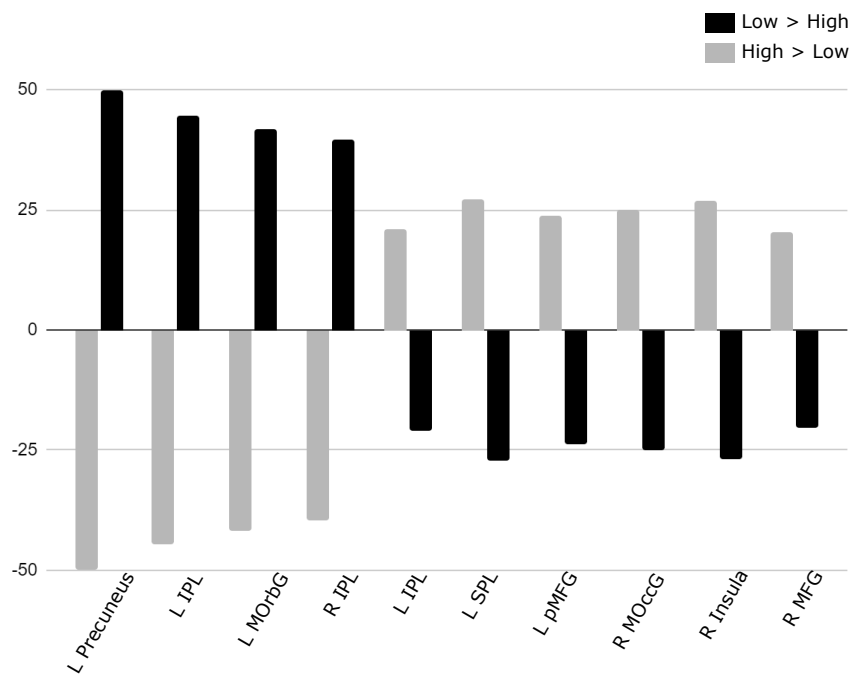


Figure B.1: **DMN and FPN Regions under Low >High and High >Low Contrasts.** Under Low >High contrast, FPN regions yielded positive activation while DMN regions were negatively activated. The opposite results were true under Low >High contrast in which DMN regions yielded positive whereas FPN regions resulted in negative activation.

Appendix C

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