PSYCHOPHYSIOLOGICAL AND FMRI RESPONSES DURING VARIOUS EXTENDED COGNITIVE TASKS: A COMPARISON OF INITIAL AND SUSTAINED ACTIVITY

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Berhan Faruk Akgür
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By Berhan Faruk Akgür

March 2025

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

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ABSTRACT

PSYCHOPHYSIOLOGICAL AND FMRI RESPONSES DURING VARIOUS EXTENDED COGNITIVE TASKS: A COMPARISON OF INITIAL AND SUSTAINED ACTIVITY

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March 2025

This doctoral thesis explores the complex dynamics of cognitive load, emphasizing its neural and psychophysiological underpinnings, with a focus on the frontoparietal multiple demand (MD) regions and the default mode network (DMN). Through a series of experiments; spanning line orientation, tactile decision-making, and auditory n-back tasks, the research investigates distinct activation patterns during task initiation and execution. By examining the complex relationship between neural activation and psychophysiological responses, particularly pupil dilation, the study reveals the multifaceted nature of cognitive load and its condition-dependent manifestations. Findings challenge the traditional view of cognitive load as a singular construct, demonstrating that it engages multiple, context-specific neural mechanisms. Nonlinear activation patterns in MD regions highlight distinct roles during task initiation and sustained engagement, while the DMN exhibits overlapping functions with MD regions, particularly during early task phases. Notably, the bilateral temporoparietal junction (TPJ) emerges as a key node, bridging traditional boundaries between these networks. Pupil dilation further mirrors these neural dynamics, underscoring its potential as a robust, non-invasive marker of cognitive load. The research contributes to a deeper understanding of how cognitive resources are dynamically allocated across varying task demands. Evidence from this interdisciplinary investigation highlights the interplay between MD and DMN regions, suggesting an integrated framework of cognitive control and self-referential processing. Insights gained extend beyond theoretical implications, offering applications in clinical settings, education,

and human-computer interaction. This includes potential advancements in diagnosing and treating neuropsychiatric disorders, optimizing cognitive training programs, and enhancing technological interfaces. By integrating neuroimaging, psychophysiological, and behavioral paradigms, this thesis provides a comprehensive account of the neural mechanisms governing cognitive load. It advances our understanding of the intricate dynamics of brain networks, offering a foundation for innovative approaches to assessing and managing cognitive demands across diverse contexts.

Keywords: Cognitive Load, Pupil Diameter, fMRI, BOLD Response, Working Memory, Multiple Demand Regions, Default Mode Network..

ÖZET

ÇEŞİTLİ UZATILMIŞ BİLİŞSEL GÖREVLERDE PSİKOFİZYOLOJİK VE FMRI TEPKİLERİ: BAŞLANGIÇTAKI VE SÜREKLİ AKTİVİTENİN KARŞILAŞTIRILMASI

Berhan Faruk Akgür
Nörobilim, Doktora
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Bu doktora tezi, bilişsel yükün karmaşık dinamiklerini, özellikle ön-paryetal çoklu talep (MD) bölgeleri ve varsayılan mod ağına (DMN) odaklanarak, nöral ve psikofizyolojik temellerini incelemektedir. Çizgi yönelimi, dokunsal karar verme ve işitsel n-back görevlerini kapsayan bir dizi deney aracılığıyla, görev başlangıcı ve yürütme sırasında ortaya çıkan farklı aktivasyon örüntüleri araştırılmaktadır. Özellikle göz bebeği genişlemesi gibi psikofizyolojik tepkilerle nöral aktivasyon arasındaki ince ilişkiyi ele alan çalışma, bilişsel yükün çok yönlü ve duruma bağlı tezahürlerini ortaya koymaktadır. Bulgular, bilişsel yükün tekil bir yapı olduğu görüşüne meydan okumakta ve bunun birden fazla, bağlama özgü nöral mekanizmayı harekete geçirdiğini göstermektedir. MD bölgelerinde gözlemlenen doğrusal olmayan aktivasyon örüntüleri, görev başlangıcı ile sürdürülen katılım sırasında farklı roller üstlendiğini ortaya koyarken, DMN'nin özellikle erken görev aşamalarında MD bölgeleriyle örtüşen işlevler sergilediği görülmüştür. İki taraflı temporoparietal bağlantı bölgeleri (TPJ), bu ağlar arasındaki geleneksel sınırları aşan önemli bir düğüm olarak öne çıkmaktadır. Ayrıca, göz bebeği genişlemesi bu nöral dinamikleri yansıtarak, bilişsel yükün güçlü ve invaziv olmayan bir göstergesi olarak potansiyelini ortaya koymaktadır. Araştırma, farklı görev talepleri boyunca bilişsel kaynakların dinamik olarak nasıl tahsis edildiğine dair daha derin bir anlayışa katkıda bulunmaktadır. MD ve DMN bölgeleri arasındaki etkileşime dair kanıtlar, bilişsel kontrol ve öz referanslı işleme için entegre bir çerçeve önermekte ve teorik çıkarımların ötesine geçerek klinik, eğitim ve insan-bilgisayar etkileşimi alanlarında uygulama olanakları sunmaktadır. Bu, nöropsikiyatrik bozuklukların teşhis ve tedavisinde ilerlemeler, bilişsel eğitim programlarının optimize edilmesi ve teknolojik arayüzlerin geliştirilmesi gibi potansiyel kazanımları içermektedir. Nörogörüntüleme, psikofizyolojik ve davranışsal paradigmaları bir

araya getiren bu tez, bilişsel yükü yöneten nöral mekanizmalar hakkında kapsamlı bir açıklama sunmaktadır. Beyin ağlarının karmaşık dinamiklerini anlamamızı ilerleterek, çeşitli bağlamlarda bilişsel taleplerin değerlendirilmesi ve yönetimi için yenilikçi yaklaşımlar geliştirmek adına bir temel sunmaktadır.

Anahtar sözcükler: Bilişsel Yük, Göz Bebeği Çapı, fMRI, BOLD Tepkisi, Çalışma Belleği, Çoklu Talep Bölgeleri, Varsayılan Mod Ağı.

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Contents

List of Figures

List of Tables

Chapter 1

General Introduction

1.1 Multiple Demand (MD) Regions

Throughout our daily lives, we encounter a continuous stream of cognitive challenges, from coordinating multiple tasks to adapting to unexpected problems. Whether making strategic decisions [9], suppressing distractions [10], or manipulating information in working memory [11], our ability to navigate complex demands relies on the brain's capacity to dynamically allocate cognitive resources [12, 13]. However, this adaptability is not rooted in a single brain region but rather in a network of frontoparietal regions known as the multiple demand (MD) regions [14, 15]. Unlike domain-specific areas dedicated to particular functions, MD regions activate across diverse cognitive tasks, regulating goal-directed behavior, cognitive flexibility, and executive control [16, 17]. Their engagement scales with task complexity, ensuring efficient coordination of mental effort in response to shifting demands [18, 19]. By understanding the mechanisms governing MD activation, we gain insight into how the brain orchestrates attention, problem-solving, and adaptation in an ever-changing cognitive landscape.

Frontoparietal regions that referred as multiple demand (MD) regions are essential for helping the mind to navigate flexible and goal directed behavior

[17, 20, 21]. MD regions, which are located across various parts of frontal and parietal cortices are highly related with a wide array of cognitive functions ranging from working memory and attentional control to decision-making and problem-solving [22, 23, 24, 25, 26, 27]. The fact that their activity responses when confronted with numerous cognitive tasks have led to their designation as multiple demand regions, highlighting their cognitive flexibility, coordinating complex cognitive tasks and critical role in responding to varying cognitive demands. This cognitive flexibility is essential because it means MD regions help us handle situations that require switching between different types of thinking or managing multiple demands at once [28]. Their importance in handling different tasks highlights their key role in our brain's ability to respond to new and changing situations.

In the past, research has closely tied higher-order cognitive functions—like cognitive control and executive functioning—to the prefrontal cortex (PFC), mainly drawing on findings from lesion studies [29, 30, 31, 32]. PFC seemed to have a crucial impact on such high order cognitive functions since the absence of it would drastically deteriorate wide range of cognitive abilities, including attention, planning, and reasoning, in other words, without a functioning PFC, a person's ability to manage complex tasks and think critically would be significantly compromised. [33, 34, 35, 36]. The introduction of neuroimaging techniques such as positron emission tomography (PET) and later functional magnetic resonance imaging (fMRI), revolutionized the understanding of certain cognitive functions, which previously believed to be emerged only or mostly from PFC. Hence, PFC believed to be the primary hub for these higher-level processes [37, 38, 39]. Current understandings revealed it's not just the PFC doing the heavy lifting. High cognitive functions are much more widely represented in the brain, they are actually distributed across a network of brain regions that span both the prefrontal cortex and parietal lobes, hence commonly refereed as frontaparietal regions or multiple demand (MD) regions, which seems to play a key role in managing and coordinating the brain's response to complex and varied cognitive tasks. [40, 17, 41]. This shift in understanding is profound. It is no longer about pinpointing the importance of one specific area like the PFC Instead, it is about recognizing how

interconnected and distributed these higher-order functions really are. The brain works in networks, and understanding those networks is crucial for getting the full picture of how we manage things like decision-making, attention, and planning in our everyday lives [42, 43].

MD regions show a broad task involvement that include wide array of cognitive tasks together instead of act as a specialized region just for a single function, which is a remarkable quality and such distinctive compare to other parts of the human body [15]. These wide array of cognitive tasks could require attention, working memory, task-switching, problem-solving, and decision-making. The concept of multiple demand regions posits that these areas form a domain-general system that supports flexible cognition by allocating neural resources based on the demands of the task at hand. [12]. This flexibility principle suggests that MD regions act distinctively different compare to more domain-specific brain areas, such as regions in the occipital cortex dedicated to visual processing or regions in the temporal lobe involved in language comprehension [12]. MD regions also show dynamic and flexible functional connectivity, which makes it possible to act interactively with other brain regions and networks depending on the task at hand, these regions ability to dynamically adjust their activity depending on the task is a very unique quality [44]. For example, during tasks requiring heightened attention and executive control that demands your full attention and requires making decisions quickly, MD regions may increase their communication with sensory and motor regions to facilitate the effective implementation of cognitive strategies, hence to help you stay sharp and act on your decisions [45, 46]. Conversely, during tasks that require introspection or self-referential thought, these regions may disengage from sensory areas and shift toward interactions with other networks, such as the default mode network (DMN) [47]. This flexibility in functional connectivity is key. MD regions don't just operate in isolation, they interact with other networks in the brain depending on what you need to do. That dynamic ability to shift gears, so to speak, is what makes these regions so essential for handling complex and varied cognitive tasks.

Cognitive flexibility is key to human thinking and cognitive processing, enabling individuals to determine and adapt their thought process and behaviors

in response to every possible task demand. The capability of shifting between various tasks, suppressing information that is redundant for the task at hand, and operate on working memory representations accordingly relies crucially on the MD regions' activity [48, 49]. MD regions show increased activity patterns when encountered with need to switch between tasks conditions or various stimuli, inhibit redundant responses, or maintaining working memory information for a limited time, in other words, MD regions kick into gear when we need to juggle multiple tasks or handle different stimuli. For example, if you're in a situation where you need to ignore irrelevant details and focus on the task at hand, or when you have to keep something in your working memory for just a short time, the MD regions are the ones stepping up. MD regions shows a consistent temporal activation pattern throughout tasks, basically, they start firing at the beginning of a task and stay active while you're working through it. It is like they are on duty the whole time you are mentally engaged. [50]. MD regions also critical for cognitive control that is crucial for goal directed tasks such as goal maintenance, goal representation, performance monitoring, conflict monitoring, error detection, and rule maintenance [51, 52, 53, 54]. MD regions are handling all that behind the scenes. Even though there are many regions that are widely distributed on various locations on frontal cortex and parietal cortex, they do not act independently from each other. This heightened connectivity supports the synchronization of neural activity required for maintaining and manipulating abstract representations in working memory. Moreover, efficient communication between MD regions could be key to facilitate the coordination of top-down control processes, enabling individuals to adapt to changing task demands and solve problems more effectively [55, 56]. Efficient communication between MD regions is critical quality that helps us stay on top of tasks, especially when the demands change or become more complex. This coordination between different parts of the brain is what helps us adapt quickly and solve problems in real time. Without that smooth back-and-forth, it would be much harder to maintain focus, switch between tasks, and make the right decisions under pressure. So, while we often take this cognitive flexibility for granted, it's actually a finely tuned system of neural connections that allows us to think and behave as effectively as we do.

MD regions show similar activation patterns when compared with activation patterns that emerge from fluid intelligence tasks. Fluid intelligence considered to be an important component of general intelligence, it plays a critical role in everyday cognitive functioning, academic performance, and success in complex tasks that require adaptive thinking [57, 58]. Fluid intelligence is linked with skills that are part of executive functions, which are essential for adapting to new environments, learning new skills, and reasoning about unfamiliar concepts, such as: problem-solving, working memory, cognitive flexibility, and abstract reasoning [14, 12, 16, 59]. Also, lesion studies revealed that damages on various MD regions impaired abilities that required flexible problem-solving and abstract reasoning, which are crucially important for fluid intelligence [29, 30, 31, 32]. MD regions selectivity in terms of regulating activity between redundant and necessary also linked with efficient neural processing that arise from higher fluid intelligence [60]. One can assume that individuals who posses higher fluid intelligence could have more optimized neural circuitry within the MD regions, allowing them to complete tasks with fewer neural resources [61, 62]. This efficiency could be due to superior connectivity within MD regions and between MD regions and other regions, more effective use of working memory, or greater flexibility in switching between cognitive strategies, all of which are critical for fluid reasoning [63]. It is expected to be a correlation with low MD activation and high fluid intelligence, since individuals who have high fluid intelligence to act efficiently with lesser neural demand, in other words, people with high fluid intelligence might use their working memory more effectively, or they may be better at switching between different cognitive strategies, depending on what the situation calls for [64, 65]. All of this is critical for fluid reasoning. Hence, MD regions are not only critical for problem-solving and reasoning but also for the broader intellectual capacity that allows us to think quickly, flexibly, and adaptively in a wide range of situations [14, 66, 67, 68].

1.2 Default Mode Network (DMN)

In moments of rest or introspection, when we disengage from external tasks, the brain does not simply shut down. Instead, it shifts to an internally focused state, engaging a specialized system known as the default mode network (DMN) [1, 69]. Whether recalling past experiences, imagining future scenarios, or reflecting on personal identity, DMN activity supports self-referential thought, mental time travel, and social cognition [70, 71]. Unlike networks involved in active task execution, DMN deactivates when attention is externally directed, allowing for a seamless transition between goal-oriented processing and internal reflection [72, 73]. However, this balance is crucial, disruptions in DMN function have been linked to cognitive disorders, where an inability to regulate its activation may interfere with task performance [6, 74]. Understanding the DMN provides deeper insight into how the brain manages the interplay between focused attention and spontaneous thought, shaping memory, creativity, and self-awareness.

Default mode network (DMN) is a large scale brain network that plays a central role and has an enormous impact on several cognitive processes [75, 76]. It has crucial influence on internally oriented cognition, which includes everything from reflecting on yourself to thinking about the past or future [77, 78]. The DMN has been heavily studied, particularly through resting-state fMRI scans, which revealed something surprising: this network becomes more active when you're not actively engaged in a specific task or when you're resting. Hence, it's called the "default mode" network, it's the brain's go-to state when it's not concentrating on the outside world. [79, 80, 81]. It was a very counter intuitive way of looking at the brain activation since it was widely assumed that brain activity was evident only while completing externally directed, effortful tasks. On the contrary, these regions exhibited synchronous activity during periods of rest, supporting the notion that the brain remains actively engaged in internally focused processes even when it is not attending to external tasks [82, 83]. The fact that the reality of DMN activation patterns towards no task conditions or rest periods revealed an astonishing new point of view on neuroscientific research, which include an understanding of the brain regions activity on conditions that

referred as inactive. Hence, DMN activity is recognized as a fundamental impact factor on various high level cognitive processes including self-referential thinking, autobiographical memory, autobiographical memory, mental time travel, theory of mind and social cognition, and spontaneous thought or mind-wandering [84, 85]. Thus, the DMN is not just a passive system that switches on when you are resting, it is actively involved in some of the most complex and important mental activities we engage in, even when we do not realize it [86]. This discovery highlighted that even when we are not focused on the outside world, our brain is still hard at work, processing information internally [87].

Self referential thinking is a representation way of thinking towards an individuals' self [88]. These self related processing may include emotions, characteristics, or future plans. It is crucially linked to sense of identity and decision making towards personal goals. Autobiographical memory arise mostly form episodic memory retrieval, which corresponds to recalling past memories that has a personal significance, remembering these moments helps to generate a sense of continuity in our lives, connecting our past selves to who we are now [89]. This process of looking back at our personal history is a crucial part of building and understanding our identity [89]. The reconstruction of such memories hold and important stage on identity formation and providing temporal continuity [90]. Then there is mental time travel, which is all about forward thinking, mental time travel is a prospective cognition that enables one to consider future possibilities [91]. It is crucial for planning, setting goals, and anticipating possible future outcomes [91]. It gives us the mental flexibility to anticipate outcomes and make decisions that are more adaptive to future challenges or opportunities, without this ability to mentally project ourselves into the future, making thoughtful, long-term decisions would be much harder [92]. Hence, it is crucial for adaptive decision making [92]. Moreover, theory of mind and social cognition are the abilities of performing complex social situation by understanding the social aspects, ideas, thoughts, and feelings of others [93, 94, 95]. When we are able to read between the lines of someone's behavior or anticipate how they might react, we are using theory of mind, it is enables the skill of empathy, navigates social behavior,

and shapes social interaction [96]. Lastly, there's mind-wandering and spontaneous thought. Mind-wandering and spontaneous thought could be seen as a negative aspect since its origin is spontaneous and depart from the task at hand [97, 98]. Surely, it can be a distraction, however it also has cognitive benefits; mind-wandering can spark imagination, help with problem-solving, and promote divergent thinking, which is the ability to come up with a wide range of ideas [99, 100, 101, 98]. Therefore, even though these thoughts seem to come out of nowhere and pull us away from what we are focused on, they can actually be quite useful when it comes to imagination and thinking outside the box [102, 103, 104]. All of these processes ,whether we are thinking about ourselves, remembering our past, imagining the future, understanding others, or letting our minds wander, are critical to how we navigate life and make decisions. They shape not just how we think, but who we are [105].

We may think of the default mode network (DMN), with all its complexities tied to high-level cognitive functions like self-reflection and social reasoning, as something uniquely human [106]. However, Humans are not the only species that rely and need a neural network such as DMN to adjust and regulate inner cognitive processes [1]. Primates, particularly monkeys, exhibit a DMN that has different anatomical boundaries and connectivity patterns than humans but in other cases very close to human DMN [107]. DMN in monkeys linked with self-monitoring, social cognition, and spatial memory [107]. These traits are crucial for monkeys to navigate in their complex social environment and critical for their spatial reasoning skills [107]. Although, monkeys inner thought patterns may not be as complicated at humans, they show a limited capacity and activation patterns related to introspective thought as humans, homologous functions in terms of social awareness and navigation of past and future scenarios, which are again contributing their survival and coping skills among their social peers [107, 108]. Also, macaque monkeys show suppression patterns while completing goal directed tasks [109, 110]. Such activity patterns suggest shifting between task positive and negative networks are not unique for humans. Interestingly, it's not just primates that possess a version of the DMN. Rodents, too, exhibit a simplified form of this network, which becomes active during rest periods, much like in humans

and monkeys [111]. However, the rodent DMN appears to be more basic and is predominantly tied to spatial memory, navigation, and contextual processing [111, 112]. It is known that rodents rely on spatial reasoning and spatial memory in many cases, it is likely that their DMN is critical on supporting their spatial skills to recall location that have food or avoid spaces that linked with danger [112]. Rodent DMN also show task negative aspects, meaning that their activity decreases when encountered with focus oriented tasks much like primates and humans [112, 113]. However, since rodent DMN is more basic then others, it is highly linked with spatial and contextual representations rather than supportive introspective and social functions [109, 110]. Even though rodents lack the introspective and social reasoning functions we see in primates and humans, their DMN still shares some core characteristics, for example, it shows task-negative features, meaning the network's activity decreases when the animal is engaged in focused tasks [111, 114]. This pattern is consistent across species—humans, monkeys, and rodents alike—which suggests that while the DMN in rodents is more limited in scope, it plays a vital role in their cognitive processing, especially in spatial tasks [111, 112, 115, 114]. So, while human introspection, social complexity, and rich internal thought patterns may stand out, we can see echoes of these processes in other species. The existence of a DMN in non-human primates and even rodents challenges the idea that this network is uniquely human [114].

The presence of DMN in different species with distinct priorities reveals that DMN is guided in a way to adjust and support the core cognitive processes of the species. Such as, in humans theory of mind, mental time travel, and self-reflection is more critical and have more representation on neural processes, hence more linked with DMN [1, 93, 94]. On primates, basic forms of such cognitive processes as humans are linked with DMN. Whereas, rodent DMN show more links with spatial memory and environmental awareness, which could be interpreted as a simpler version of human and primate DMN [111, 114, 116]. Altogether, DMN is present to serve key cognitive functions across a variety of species [116].

A defining aspect of DMN is the activity decrease when encountered with externally directed activities that are focused on task at hand. This deactivation of DMN emerge as activation on task positive networks such as multiple

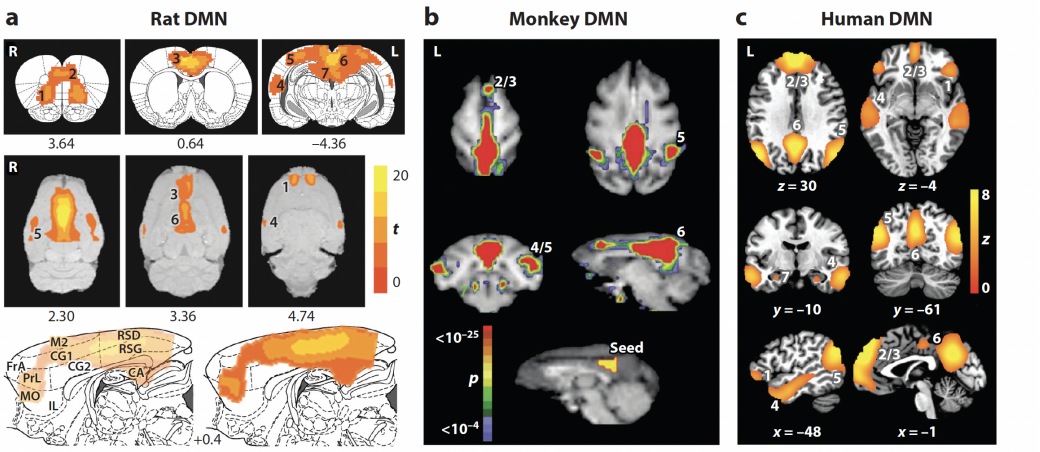

Figure 1.1: Current figure shows the comparison of DMN activity on a) rat brain b) monkey brain c) human brain [1]

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demand (MD) regions [1]. It is expected that in order to direct ones focus on a specific matter, one need not focus on redundant aspects. Deficits on suppressing DMN activity is linked with several cognitive dysfunctions including obsessive compulsive disorder (OCD) attention-deficit/hyperactivity disorder (ADHD) and schizophrenia [117, 118]. In essence, the balance between the DMN and task-positive networks like the MD regions is crucial. When functioning properly, it allows us to switch between internally focused thinking and external tasks smoothly. But when that balance is disrupted, as we see in certain cognitive disorders, it becomes much harder to maintain attention and regulate thought processes effectively. [119, 120].

The DMN is originated from anatomically distinct set of regions that are functionally closely connected [121]. These interconnected composed regions form a unified system, collectively orchestrating its functions. In other words, DMN operates as a cohesive unit, exhibiting highly synchronized activity, particularly during states of rest or when attention is directed internally [122]. DMN becomes active when we are not actively focused on the outside world. Therefore, it increase activity when one is engaged in tasks that involve introspection, self-referential thought, or the recalling of personal memories. These activity patterns are related with certain cognitive concepts such as mind-wandering, daydreaming,

and spontaneous thought generation [123, 124, 125]. While DMN shows deactivation patterns on interactive and focus oriented tasks such as external tasks or goal-directed tasks; its intrinsic activity during rest and passive states suggests that the brain is never truly at rest [126, 127, 128, 81, 129]. On the contrary, DMN is regularly active, aiming to maintain many baseline cognitive functions and facilitating the processing of internally directed thoughts. DMN appear to be related with many fundamental aspects of cognitive process such as consciousness, identity, and mental health [129]. DMN's steady rhythm is crucial for our mental health and overall cognitive functioning. Without this network, some of the core aspects of what makes us human—like consciousness, self-awareness, and even mental wellness—might be at risk [74]. So, while it's easy to think that our brains only work when we're actively engaged in a task, the DMN tells a different story. Even when you're daydreaming or lost in thought, there's a lot happening under the surface. Hence, the brain never truly rests, it's always churning through layers of internal processing that are just as important as the things we're conscious of doing [124, 74].

The DMN stands out because of the way it shifts gears depending on where our focus is directed. When we are engaged in tasks that require a lot of external attention, like solving a problem, or paying close attention to something, the DMN tends to "quiet down", deactivating to make room for brain regions that are more suited to handling those immediate demands [130, 131]. But as soon as our attention turns inward—whether we're reflecting on our own thoughts, daydreaming, or recalling memories—the DMN comes back online [124]. This ability to switch between "resting" and "active" states highlights the DMN's role in balancing the internal and external worlds. It's not just about spacing out or being on autopilot; the DMN helps regulate the brain's shift between states of focus and relaxation, keeping the balance between our inner narrative and the task at hand [6]. This makes it a central player in managing how we process information, both cognitively and emotionally; whether we are thinking about ourselves, processing emotions, or reflecting on a past experience, the DMN is involved in guiding that mental flow, helping us transition seamlessly from one type of thinking to another [1, 132].

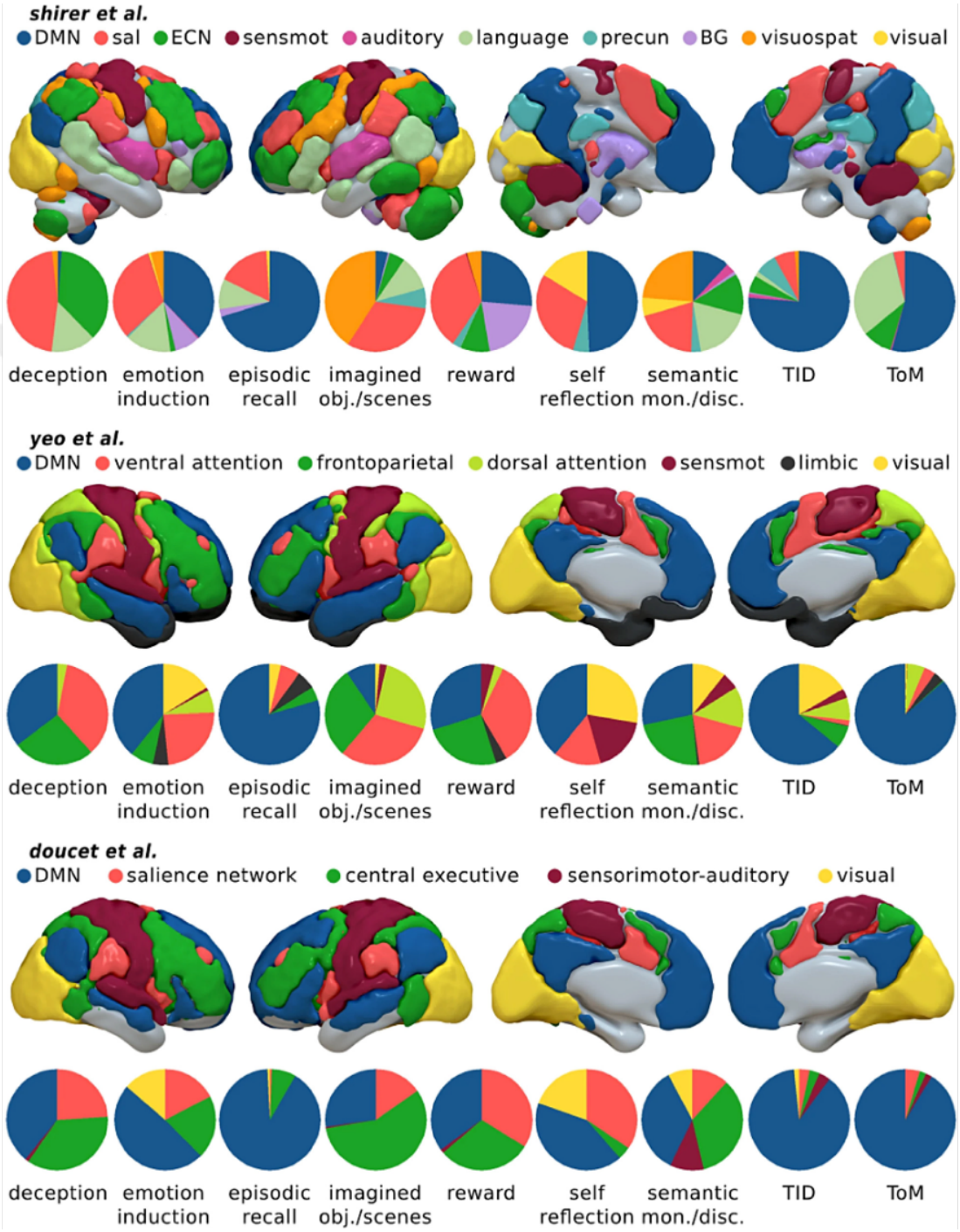

Figure 1.2: Various cognitive functions that are linked with several brain networks shown. Concepts include task-related deactivations, understanding others' thoughts, word meaning differentiation, memory recall, emotional response, and self-awareness. The percentage of brain areas that are linked with certain cognitive abilities and brain networks are presented with their association of the the default mode network (DMN). The compared major brain networks include the executive control network (ECN), frontoparietal control network, salience network, precuneus, basal ganglia, visuospatial network, and sensorimotor network. Task-induced deactivations (TIDs) refer to brain regions that become less active during tasks. [2, 3, 4, 5, 6]

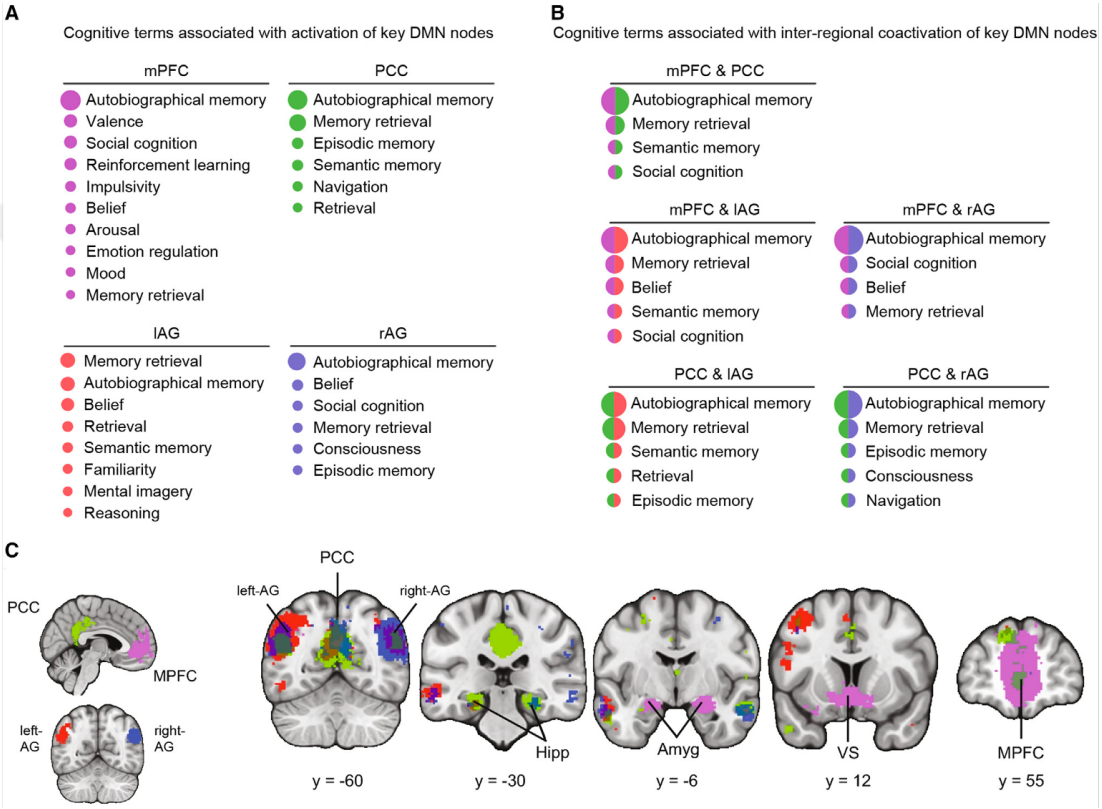

Figure 1.3: (A) Cognitive functions linked to the activation of the mPFC, PCC, and left and right angular gyrus (AG) nodes of the DMN, based on data from 14,000 task-related studies. The log-odds ratio (LOR) reflects the likelihood of a cognitive term being mentioned. (B) Cognitive functions associated with the coactivation of the mPFC, PCC, and left and right AG nodes of the DMN, analyzed in pairs. The data were generated using NeuroLang (https://neurolang.github.io/). (C) A meta-analysis of task-related coactivation patterns of the mPFC, PCC, and AG reveals that the PCC and mPFC exhibit strong coactivation. The mPFC shows coactivation with both the amygdala and ventral striatum, while the left AG coactivates with the left MTG. The PCC, in turn, is uniquely coactivated with the hippocampus. Hipp refers to the hippocampus; Amyg to the amygdala; and VS to the ventral striatum. [7, 6]

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1.3 Cognitive Mechanisms and Extended Tasks

While execution of tasks that have a higher complexity, during the initial stages, when multiple cognitive mechanisms are concurrently active, the demand on cognitive resources intensifies, leading to a decline in overall performance, delayed cognitive processing, and heightened proneness to errors. Such as, a task that requires divided attention, results in a performance decrease because of the overall complexity of required task demands not because of real time target processing [16]. Importantly, it generates characteristic signatures in psychophysiological markers and neural activity [133, 134].

Extended tasks, characterized by the simultaneous execution of multiple complex actions, impose a substantial cognitive load due to the intricate management of various tasks and their associated demands [135]. When individuals engage in such extended tasks, their cognitive processes perceive and treat them as cohesive and indivisible units, as opposed to discrete and separate actions. This cognitive integration is facilitated by the activation of specialized cognitive mechanisms that harmoniously organize, integrate, and regulate the multitude of constituent acts, allowing for seamless execution. We may prepare dinner or write a Ph.D. thesis, and not individually execute the very many acts that constitute these tasks [136]. These observable behaviors serve as indications of the activation of specific cognitive mechanisms that encompass the entire temporal span of the task. In other words, specific cognitive mechanisms manifest as integral components within a larger ensemble of goal-directed modifications transpiring throughout the task duration [14]. Extended tasks necessitate a continuous task focused attention, systematically foregrounding pertinent memories, predictions, skills, and dispositions [12, 137]. This dynamic orchestration ensures that at any given point within the task, cognitive processes attain an optimally adaptive state tailored to the anticipated demands [138, 14]. These cognitive mechanisms are evidenced by characteristic behavioral signs at task beginnings [139] and by characteristic neural signs at task completions [136].

The instantiation of larger and more complex cognitive mechanisms for extended tasks places a greater demand on cognitive resources [140]. However, there is a constraint on the size of mechanisms that can be concurrently instantiated. Consequently, longer and more complex tasks are executed as a series of minor tasks, each governed with a less complex process [136]. In other words, we tend to break down larger tasks into smaller, more manageable parts. Each of these smaller tasks is handled by simpler cognitive processes. For example, when writing a research paper, we may break it down into smaller tasks like researching, outlining, drafting, and editing, rather than trying to tackle the whole process at once [141, 139]. While the neural and psychophysiological responses to the demands of instantiating such complex cognitive mechanisms remain unknown.

As an extended task unfolds and its constituent actions are performed in sequence, the cognitive load required for the task shifts and diminishes progressively [142]. Initially, when we start an extended task, a wide range of cognitive processes are activated, engaging multiple mental resources to ensure smooth and organized execution [140]. These processes include not only basic attention and memory systems but also more complex mechanisms such as planning, decision-making, and the integration of various sensory and motor functions [14].

At the onset of any task, the brain operates at a heightened level, akin to laying down a mental blueprint for the sequence of actions required to complete the task. During this phase, the structure of the task is actively established, with cognitive mechanisms determining the necessary steps, goals, and sequences to ensure a smooth progression [143, 144]. This process can be likened to preparing for the construction of a complex project, where all tools must be gathered, plans carefully laid out, and the role of each component clearly understood before actual execution begins. At this initial stage, the brain is required to thoroughly process and account for every aspect of the task, resulting in a peak cognitive load [9]. The mental effort expended during this period is significant, as the individual is managing a large amount of information, recalling and organizing relevant details, and ensuring that each component is approached in the appropriate order [11]. This activation phase places considerable demands on cognitive resources, as multiple processes are being initiated and coordinated [145]. Once

this foundational setup is completed, the cognitive load begins to diminish as the task progresses and becomes more routine. However, during this early phase, the cognitive effort is intensified as the brain works to organize and prepare for the task's execution [146].

At the outset of a task such as meal preparation, the cognitive demands extend beyond the physical act of cooking. During this initial phase, the focus is primarily on planning. Decisions must be made regarding the selection of ingredients, their locations, and the sequence of actions required to successfully execute the dish [136, 147]. At this stage, the brain is heavily engaged, synthesizing and storing relevant information, such as ingredient lists, in working memory for rapid access when needed [148]. Cognitive resources are actively deployed, shifting attention between the recipe, locating items in the kitchen, and ensuring the correct utensils are prepared. In this early phase, attentional resources are distributed across multiple stimuli, requiring careful management [149]. The brain operates as though maintaining a mental checklist, coordinating different pieces of information while simultaneously ensuring that no detail is overlooked [150]. From a cognitive perspective, this stage engages a broad array of mental resources, leading to heightened cognitive load. The individual is not only considering what needs to be done, but also actively coordinating multiple actions, managing attention across various tasks, and organizing all necessary elements into a coherent plan, which results in peak cognitive load, as the brain is tasked with managing a high volume of information before the cooking process has even begun [151].

As the task progresses, certain cognitive processes that were initially critical, such as recalling specific ingredients or their locations, gradually become redundant [143]. Once the necessary ingredients have been gathered, the mental resources allocated to this phase of the task are no longer required. The brain, recognizing that these particular cognitive demands have been satisfied, adapts by reducing the attentional load associated with them [11]. The mental representation of where the flour is stored or how much oil is needed becomes irrelevant, as the task has been successfully completed. At this juncture, cognitive resources are either reallocated to subsequent stages of the task or conserved for later use

[152]. The shift in cognitive load reflects an inherent efficiency in how the brain manages resources, allowing attention to be redirected toward more immediate demands [153]. This dynamic adjustment ensures that unnecessary information is no longer occupying valuable mental space, enabling the individual to focus on the next steps in the task without the burden of maintaining redundant details. Thus, the brain demonstrates a fluid and adaptive process, seamlessly transitioning from one cognitive focus to another as the task unfolds [147].

Hence, as tasks unfold, particularly those that can be divided into distinct, manageable components, cognitive load tends to decrease incrementally as each specific element is completed. Once a particular phase of the task, such as gathering ingredients, is finished, the brain naturally redirects its cognitive resources to the next phase, such as chopping or mixing [135]. This shift allows for a more efficient distribution of mental effort as the task progresses. [135, 154]. In our example, after the ingredients are gathered, the cognitive demands associated with recalling where they are stored or how much is needed are no longer relevant. These task-specific mental representations recede into the background, freeing up cognitive potential [155]. The brain, in turn, reallocates its attention to the next task, such as preparing the ingredients. In this way, cognitive resources are dynamically managed, ensuring that mental effort is directed toward the most immediate and pressing demands of the task at hand [153]. This fluid adjustment in cognitive load is a reflection of the brain's capacity to optimize task performance, allowing for sustained focus without overwhelming the limited pool of mental resources [156]. As each phase of the task concludes, the burden tied to its completion diminishes, creating space for more efficient engagement with subsequent steps, ultimately leading to a smoother, more organized workflow [150].

In essence, the brain continuously recalibrates its distribution of cognitive resources in response to the evolving demands of a task. This dynamic allocation ensures that once a particular action has been completed, the cognitive elements associated with it no longer occupy valuable space in working memory or attentional focus [155, 156]. By offloading irrelevant information, the brain effectively streamlines cognitive processes, allowing for more efficient task execution [135].

As the task progresses, fewer cognitive resources are required, as certain components either become automated or are fully completed [153]. The brain's ability to gradually reduce the cognitive load reflects an adaptive mechanism, one that optimizes mental effort by prioritizing the steps that remain [150]. This recalibration allows for sustained cognitive efficiency, minimizing the risk of overload, and ensuring that attention remains focused on the critical elements necessary for task completion. In this way, the brain's cognitive economy allows for a seamless transition between task phases, reducing unnecessary mental effort while maintaining effective performance. Thus, leaving only the remaining steps in focus [154].

Consequently, the cognitive mechanisms engaged in task execution are most fully activated at the outset, when the task demands not only an overarching plan but also active engagement with each discrete component of the process [155, 156]. At this initial stage, the cognitive load is at its highest, as the brain is required to manage and integrate multiple elements simultaneously [143]. However, as the task unfolds and individual components are successfully completed, the cognitive burden associated with them diminishes [153]. This progressive reduction in cognitive load allows for a more efficient allocation of mental resources as the task moves forward [154]. By the time the task nears completion, the cognitive demands have significantly lessened, with only a fraction of the original mental effort remaining [150]. At this stage, the brain is primarily focused on the final steps required to bring the task to a conclusion. This gradual decline in cognitive load reflects the brain's capacity to optimize its resources over time, concentrating effort where it is most needed and reducing unnecessary cognitive engagement as elements of the task are resolved [135]. Such efficiency not only enhances task performance but also prevents cognitive fatigue, ensuring sustained focus until the task is fully completed [153, 154, 139, 157].

This natural progression of cognitive load, starting high and tapering off as certain portions of tasks are completed, reflects the brain's ability to conserve mental energy and optimize performance over time [157]. It also helps explain why extended tasks, while initially demanding, become easier to manage as they unfold, with complex cognitive operations becoming unnecessary once initial planning

and organization are complete. Understanding this cognitive mechanism can be crucial in designing more efficient workflows, training programs, or even learning strategies, as it highlights the importance of front-loading mental effort and progressively reducing it as tasks become routine or automated.

1.4 Pupil Dilation as Psychopyhsiological Representations of Cognitive Demands

Similar to the way physical load is accompanied by physiological changes, mental load is also accompanied by physiological changes [158]. Some of the well-characterized psychophysiological changes involve pupil diameter, sweating, heart-rate and heart-rate variability. Researchers tried to monitor heart rate and detect small changes of heart rate [159]. However, heart rate monitoring showed intrusive and inaccurate on detecting cognitive load, which showed redundant activity [160]. Whereas pupil dilation could be a sufficient measurement on distinguishing high and low cognitive load up to 75%, which is a higher percentage than skin conductance, respiration, cardiac measures, and eye blinks [161].

At its core, pupil dilation serves fundamental optical functions, regulating the amount of light entering the eye to optimize visual acuity and sensitivity across varying illumination levels [162]. Under bright lighting conditions, the pupil constricts, reducing the influx of light to prevent overexposure and maintain optimal visual clarity. Conversely, in dimly lit environments, the pupil dilates, maximizing light intake to enhance visual sensitivity and facilitate perception in low light conditions [162]. This dynamic regulation of pupil size, orchestrated by the intricate interplay of sympathetic and parasympathetic nervous system activity, exemplifies the adaptive nature of the human visual system in optimizing sensory input for efficient information processing [8].

Pupil dilation, defined as the involuntary expansion and contraction of the pupil, is a remarkable physiological phenomenon that serves a variety of functions,

extending far beyond its superficial anatomical characteristics. Often overlooked as merely a physical attribute, the dynamic variability in pupil size reveals its significant role as an insightful reflection of the intricate processes occurring within the human mind and body. In a range of contexts, pupil dilation emerges as a reliable indicator of cognitive engagement, emotional states, and physiological arousal. When individuals encounter stimulating stimuli or engage in demanding cognitive tasks, the autonomic nervous system responds by facilitating pupil dilation, a reaction that signifies heightened attentional focus and information processing [163]. This correlation between pupil size and cognitive load has been well documented, indicating that changes in pupil diameter can offer valuable insights into the complexity of cognitive efforts [164]. Moreover, pupil dilation serves as a key barometer of emotional arousal, reflecting the interplay between cognitive appraisal and physiological response [165]. Research has shown that emotional stimuli, whether they provoke fear, excitement, or interest, can lead to significant changes in pupil size, thereby linking emotional states to physiological manifestations [166]. This dynamic relationship between the brain and body underscores the importance of pupil dilation as a tool for understanding how individuals navigate their internal and external environments. In essence, pupil dilation acts as a sophisticated physiological marker that encapsulates the complexities of human cognition and emotion, offering researchers and practitioners alike a window into the underlying mechanisms that govern our responses to both the world around us and our internal experiences. [167, 168, 169, 170].

As mentioned, pupil dilation emerges as a sensitive marker of emotional arousal and affective processing, reflecting the autonomic modulation of emotional responses by the central nervous system. Across a spectrum of emotional experiences, from fear and anxiety to joy and excitement, alterations in pupil size serve as a reliable index of emotional reactivity and physiological arousal [168]. The sympathetic arousal associated with emotional states elicits dilation of the pupil, mediated by the release of neurotransmitters such as norepinephrine and the activation of subcortical structures implicated in the regulation of emotional responses [167]. Thus, pupil dynamics offer a non-invasive window into the subjective experience of emotions and provide valuable insights into the underlying

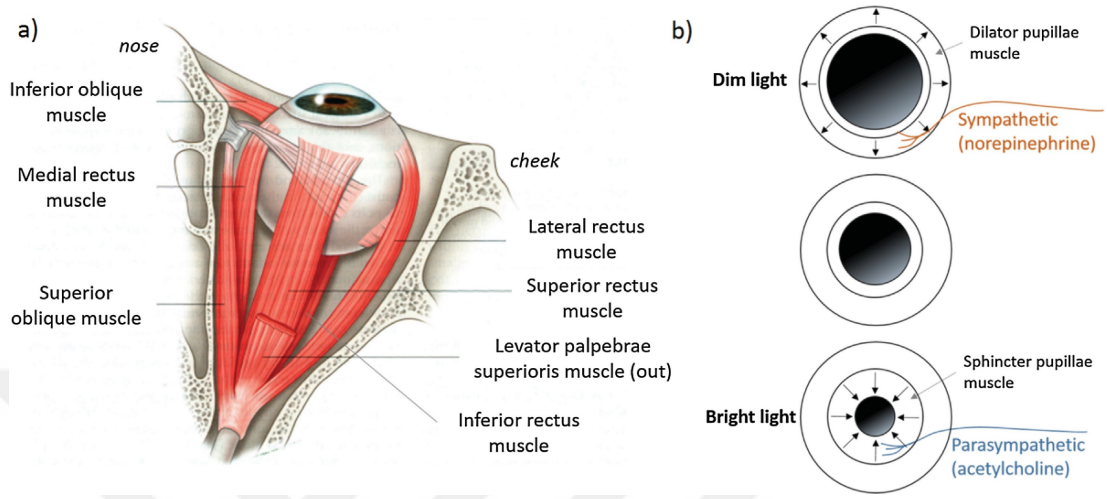

Figure 1.4: a) Muscles surrounding the eye are shown. b) Pupillary response to light is shown, including sympathetic (norepinephrine) and parasympathetic (acetylcholine) system involvements [8]

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neural mechanisms governing affective processing [171]. Furthermore, The bidirectional transaction between pupil dynamics and autonomic arousal underscores the intricate connections between the brain, body, and environment, highlighting the holistic nature of psychophysiological functioning [8].

Pupil dilation serves as a reliable index of cognitive engagement and mental workload, reflecting the dynamic allocation of attentional resources during cognitive tasks [164, 158, 163]. Research spanning cognitive psychology, neuroscience, and human-computer interaction has consistently demonstrated the tight coupling between pupil size and cognitive processes such as attention, arousal, and cognitive effort [172]. During tasks requiring heightened cognitive demands or sustained attention, pupil dilation tends to increase [168, 173, 168], mirroring the recruitment of cognitive resources and the engagement of higher-order neural circuits involved in task performance [174]. Conversely, states of cognitive fatigue or reduced attentional focus are often accompanied by pupil constriction, indicative of decreased cognitive load and arousal levels [175, 176, 177].

In other words, pupil dilation has long been acknowledged as an index of heightened cognitive demands, including augmented working memory loads [178, 179].

The expansion of pupil diameter serves as a proxy for the mental effort and cognitive resources required to accomplish the task at hand [180]. It is crucial to have an independent measure in order to differentiate mental effort levels of individuals [180]. Specifically, in the domain of working memory, various demands influence the load [181, 11], encompassing factors such as the number of items to be remembered for subsequent tasks, the number of items relevant to the current task, and the interference arising from items associated with different tasks [180]. Pupil size serves as a manifestation of the activity of modulatory systems, such as the locus coeruleus situated in the brain stem, which exert diffuse projections onto the cortex [182, 183, 184]. Thus, pupil diameter represents a valuable psychophysiological measure, not only for assessing working memory load but also for exploring various other cognitive processes, including task switching, response inhibition, memory recall, exploration and attentional detection [185, 186, 187, 180].

Hence, pupillary response reflecting the intricate modulation of autonomic nervous system activity by higher-order cognitive processes [188]. Recent advancements in pupillometry techniques have enabled researchers to dissect the fluctuations in pupil size with unprecedented precision, unveiling its potential as a reliable biomarker for cognitive engagement, emotional reactivity, and even pathological states [189, 173, 190, 191, 192, 193, 194].

1.5 fMRI Activation as a Representation of Cognitive Demands

Meanwhile psychophysiological techniques are good representations of cognitive performance [189, 173, 190], fMRI has revolutionized our ability to non-invasively map the functional architecture of the human brain [195, 196], allowing for the delineation of neural circuits underlying diverse cognitive functions. By detecting changes in blood oxygenation levels, fMRI provides a surrogate measure of neural activity with high spatial resolution, enabling researchers to pinpoint the brain regions implicated in specific cognitive tasks or psychological states [197, 198].

In the realm of neuroscience, understanding the relation between psychophysiological responses and brain activity holds profound implications for unraveling the mysteries of human cognition and behavior [199]. Among these responses, pupil dilation has emerged as a fascinating avenue of investigation, offering a window into the underlying neural mechanisms orchestrating cognitive processes. Concurrently, functional magnetic resonance imaging (fMRI) stands as a cornerstone technology, allowing researchers to probe the neural substrates of various cognitive functions with unparalleled spatial resolution [200]. To illuminate the underlying neural circuitry and shed light on the functional significance of these physiological markers in cognitive processing. Integrating methodologies from psychophysiology and neuroimaging, it is possible to provide a holistic understanding of how psychophysiological responses, particularly pupil dilation, relate to the activation patterns observed in the human brain [167, 201, 180].

The exploration of brain networks and their functional significance has been a central theme in neuroscience for decades, early neuroanatomical studies laid the groundwork for understanding the structural connectivity within the brain, highlighting the importance of distinct regions and their interactions in supporting various cognitive functions [202, 203, 204, 205, 206, 207, 208]. With the advent of non-invasive neuroimaging techniques such as functional magnetic resonance imaging (fMRI), researchers gained insights into the dynamic patterns of neural activity underlying cognition [209, 38]. This technological revolution paved the way for the discovery and characterization of large-scale brain networks, including the frontoparietal multiple demand (MD) regions and the default mode network (DMN).

The human brain is a marvel of complexity, comprising complex networks of interconnected regions that orchestrate a myriad of cognitive processes essential for adaptive functioning in the dynamic world. Among these networks, the frontoparietal MD regions and the default mode network (DMN) emerge with critical importance, each contributing distinct yet complementary functions to the cognitive architecture of the brain [75, 47, 210, 211]. Understanding the roles of these networks provides critical insights into the neural substrates underlying diverse cognitive functions, from goal-directed attention and executive control to

self-referential thought and social cognition.

At the forefront of cognitive control and executive functioning lie the frontoparietal MD regions, encompassing a distributed network of cortical areas spanning the frontal and parietal lobes. This network, often referred to as the multiple demand (MD) regions, exhibits remarkable flexibility and adaptability, dynamically reallocating cognitive resources to meet the demands of varying task contexts [212]. Across a spectrum of cognitive domains, including working memory, attentional control, and decision-making, the frontoparietal MD regions play a central role in coordinating goal-directed behavior, inhibiting irrelevant information, and flexibly updating cognitive representations in response to changing environmental demands [213, 214, 215]. This network's functional versatility underscores its critical importance in orchestrating adaptive responses to complex cognitive challenges, from mundane everyday tasks to high-level problem-solving scenarios [216].

Cognitive control plays its critical role in managing heightened cognitive demands [217]. MD regions are involved in this cognitive process. These regions include the inferior frontal sulcus, anterior insula, intraparietal sulcus, and anterior prefrontal cortex. They exhibit discernible activation patterns in response to increased cognitive demands, particularly when confronted with tasks that necessitate augmented working memory load [14, 218]. These frontoparietal (MD) regions are instrumental in attentional control and the execution of goal-directed activities across a range of cognitive tasks [219].

In contrast to the externally-oriented cognitive processes mediated by the MD regions, DMN governs introspective and self-referential aspects of cognition, encompassing a distributed set of brain regions that deactivate during externally-focused tasks and activate during rest or internally-directed mental processes [220, 75, 113, 6]. DMN encompassing the anteromedial prefrontal cortex, posterior cingulate cortex, and temporoparietal junctions, have been linked to various cognitive processes, including stimulus-independent thought and mind wandering, which tend to increase when individuals are not actively engaged in specific tasks [73, 221, 222, 223, 224, 72, 225]. Additionally, default mode network contribute to

scene construction, self-projection, and the recollection of past experiences, further supporting their involvement in mind wandering during rest [226, 227, 71]. However, it should be noted that these regions are not exclusively associated with rest-related processes, as they also play a role in task-relevant functions such as motor planning [47, 228].

The cognitive load or task difficulty that leads to deactivation in default mode regions is determined by the length and complexity of the overarching task in which cognition is currently engaged, rather than the complexity of individual component actions [229, 230]. This load does not specifically pertain to the demands of the ongoing action itself, but rather reflects the requirements imposed by the larger task in which the behavior is embedded. For instance, longer attentional tasks, expected to persist for 40 seconds, induce greater deactivation in default mode brain regions compared to shorter attentional tasks lasting only 20 seconds [231]. Recent research challenges the notion that task-related deactivations occur exclusively within predetermined regions and suggests that such deactivations can manifest in any region not currently engaged in a specific task, contradicting theories proposing an anti-correlation between MD and DMN regions [231]. The extent of deactivation in various brain regions, including those within the default mode network, correlates with the size or load of active cognitive mechanisms [231].

Notably, the deactivation observed in brain regions known to deactivate in response to cognitive load tends to be most pronounced at the initiation of extended tasks and gradually diminishes as the task progresses, with activity eventually returning to baseline levels towards the task's conclusion, furthermore, programs associated with longer tasks are anticipated to be larger in scale [231]. Consequently, program-related deactivation within these regions is particularly prominent at the outset of longer tasks [231].

The dichotomy between the MD regions and the DMN reflects the brain's intrinsic balance between externally oriented attentional control and internally directed self referential processing. While the MD system mobilizes cognitive resources to navigate the external environment and achieve goal-directed behaviors

[215], the DMN facilitates introspective processes that underlie self-awareness, social understanding, and autobiographical memory [232]. Importantly, these networks do not operate in isolation but engage in dynamic interactions and functional coupling, reflecting the brain's capacity for integrated information processing across diverse cognitive domains [233, 234].

While traditionally viewed as distinct entities with opposing functions, MD regions supporting externally oriented tasks [235] and the DMN subserving internally directed processes [236], our study suggests a more interactive relationship between these networks. Intricate patterns of connectivity and functional dynamics that challenge the dichotomous view of brain function. MD regions and DMN engage in dynamic interactions, exhibiting both antagonistic and synergistic relationships depending on task demands and cognitive states [237].

Moreover, dysregulation or aberrant functioning of these networks has been implicated in various neuropsychiatric disorders, underscoring their clinical relevance and translational significance. Alterations in the frontoparietal MD network have been associated with deficits in executive functioning observed in conditions such as attention deficit hyperactivity disorder (ADHD), schizophrenia, and traumatic brain injury [238]. Similarly, disruptions in the DMN have been linked to disorders characterized by aberrant self-referential processing, including depression, bipolar disorder, autism spectrum disorders, Alzheimer's disease, substance usage, and addiction [239, 240, 241, 242].

In summary, elucidating the functions of the MD regions and the DMN provides a foundational framework for understanding the neural basis of cognition, consciousness, and self-awareness. By unraveling the interactions between these networks and their role in mediating diverse cognitive processes, researchers can gain deeper insights into the nature of human cognition and its underlying neural substrates, with implications for both basic neuroscience research and clinical interventions targeting neuropsychiatric disorders.

1.6 Hypotheses and Aims

This thesis contributes to the growing body of research on cognitive control and neural mechanisms of task execution by providing a detailed examination of how multiple demand (MD) regions and the default mode network (DMN) interact during extended cognitive tasks. Through a combination of fMRI and psychophysiological measures, it explores the role of MD regions in cognitive flexibility, executive control, and problem-solving while also investigating how DMN deactivations are modulated by task demands. A key contribution is the identification of distinct activation patterns between task initiation and sustained engagement, suggesting that cognitive load is not a unitary process but rather comprises multiple overlapping mechanisms that vary in complexity and resource allocation. Additionally, this work advances the understanding of pupil dilation as a psychophysiological marker of cognitive load by demonstrating its strong correlation with MD activations. By addressing gaps in current literature, particularly the assumption that MD and DMN operate in strict opposition, this thesis proposes a more dynamic framework in which certain DMN regions, such as the temporoparietal junction, exhibit functional overlap with MD regions under specific conditions. The findings have implications for neurocognitive models of cognitive control, fluid intelligence, and task adaptation, with potential applications in clinical interventions, education, and human-computer interaction. Overall, this research deepens our understanding of the neural architecture supporting adaptive cognition and highlights the intricate balance between brain networks in managing complex, goal-directed behaviors.

Thus, the present study aims to deepen our understanding of the neural mechanisms underlying cognitive load and task difficulty, particularly focusing on the frontoparietal multiple demand (MD) regions and the default mode network (DMN). By examining distinct activation patterns at the beginning and during task episodes, this research investigates how varying levels of cognitive demand impact these regions [12]. The study also seeks to explore the relationship between fMRI activations and psychophysiological markers, specifically pupil dilation, to determine their accuracy as proxies for neural activity in cognitive load processing

[243, 244, 245]. The experimental designs include a line orientation experiment, a tactile decision making experiment, and a auditory n-back experiment. all encompassed extending tasks, each with distinct levels of complexity. Extensive empirical evidence supports the notion that increase in the difficulty engenders heightened activation within MD regions associated with cognitive control, as evidenced by the phenomenon of pupil dilation [246, 247, 248, 249, 250].

Three primary hypotheses guide this investigation. Firstly DMN and MD network activations may overlap in unexpected ways. Contrary to views that segregate the MD regions and DMN, this hypothesis proposes, since certain brain regions such as extrastriate cortex can act as a part of MD regions [251], certain DMN regions (such as the temporoparietal junction, TPJ) can act with activation patterns more similar to MD regions rather than DMN. This challenges the conventional understanding of these networks as functionally distinct, suggesting instead that there may be greater overlap in their role during complex cognitive tasks, particularly during the initial stages of cognitive engagement.

Secondly, pupil dilation acts as a robust psychophysiological marker of brain activity. This hypothesis suggests that pupil dilation should be closely aligned with fMRI activations in MD regions, particularly reflecting cognitive load or task difficulty. The observed similarity between pupil dilation trends and MD activation patterns implies that psychophysiological responses like pupil dilation can serve as precise indicators of brain activity. This finding highlights the potential for pupil dilation to offer a reliable and non-invasive measure of neural processes related to cognitive load and task difficulty.

Lastly, Cognitive load is not a unitary construct. The hypothesis posits that cognitive load engages multiple, distinct neural mechanisms, which should be evidenced by nonlinear fMRI activation patterns in MD regions. Specifically, fMRI activations in the MD network differ between task beginnings and task engagement across different difficulty levels. This would suggests that cognitive load is not a single, uniform process but instead reflects multiple overlapping cognitive mechanisms depending on the stage of task performance and level of difficulty. Furthermore, anticipated findings suggest that the more complex tasks

will evoke pronounced activation within MD regions in comparison to the simpler task. Such heightened neural activity reflects the augmented cognitive load and the engagement of cognitive control mechanisms requisite for successful execution of the more intricate cognitive mechanism. It is possible that the execution of challenging extended tasks requires two different cognitive processes such as a cognitive process instantiated at the outset (beginning) and a set of control processes instantiated subsequently (main task). If these two types of cognitive processes differ, then easy and difficult extended tasks should manifest distinct characteristics at their initial step, when cognitive mechanisms are instantiated, compared to later steps through these cognitive mechanisms. While the latter is well-established to activate MD regions, the former is posited to decrease activation or deactivate them. This hypothesis is empirically tested across four distinct experiments.

The cognitive load engendered by extended tasks arises from the intricate orchestration of multiple actions as an integrated and indivisible unit. The activation of cognitive mechanisms at the task's inception, encompassing the entire duration, sets the stage for efficient task execution. Subsequently, as different segments of the task are completed, the cognitive mechanisms progressively diminishes, optimizing the allocation of cognitive resources. A comprehensive understanding of these intricacies surrounding cognitive load in extended tasks can inform the development of strategies aimed at optimizing task performance and mitigating cognitive overload.

In the light of these multifaceted functions, pupil dilation emerges as a versatile and sensitive biomarker with far reaching implications for research domains ranging from neuroscience and psychology, through a comprehensive investigation of the relationship between pupil diameter and neural responses at the outset of the more complex tasks, we aim to unravel the relation between psychophysiological and neural markers of cognitive load. Such an in depth understanding of these disparities and associations has the potential to furnish valuable insights into the underlying cognitive processes that govern the initiation of extended tasks. Moreover, it has the capacity to shed light on the dynamic nature of cognitive control and the efficient allocation of cognitive resources in response to variations

in task complexity.

Furthermore, The complex relation between the multiple demand regions and the default mode network, has the potential to shedding light on their reciprocal influence and functional significance in human cognition. By employing a multidisciplinary approach encompassing neuroimaging techniques and behavioral paradigms, this research seeks to elucidate the underlying mechanisms governing their coordination and cooperation, therefore, constructing a deeper appreciation of the remarkable complexity of the human brain.

These findings have the capacity of increasing our understanding of brain function and cognition towards to applications in clinical settings, education, and human computer interaction. Insights into the neural substrates of cognitive control and self referential processing may inform the development of targeted interventions for neuropsychiatric disorders characterized by dysfunctions in these processes, such as attention deficit hyperactivity disorder (ADHD), schizophrenia, and depression. Nevertheless, a deeper understanding of MD regions and DMN interactions could inform the design of cognitive training programs and assistive technologies aimed at enhancing cognitive abilities and fostering resilience in healthy individuals and clinical populations.

In conclusion, the proposed doctoral thesis seeks to advance our knowledge of the MD regions and the DMN, elucidating their reciprocal influence and functional significance in human cognition through a comprehensive and interdisciplinary approach. By integrating neuroimaging techniques, psychophysiological and behavioral assessments, this research aims to unravel the complex dynamics of brain networks and pave the way for innovative approaches to understanding and enhancing cognitive function.

Chapter 2

Line Orientation Pupil Dilation Experiment

2.1 Introduction

The overarching objective of our study is to investigate how the complexity of cognitive tasks influences psychophysiological markers, particularly focusing on pupil diameter, within the context of extended task performance. Specifically, we aim to understand how variations in working memory load impact pupil dilation responses during the execution of tasks that require sustained cognitive engagement over time. To achieve this, we manipulate the working memory load experienced by participants during extended task sessions. By varying the complexity of the task, particularly in terms of the number of line orientations that need to be retained and recalled, we aim to discern how changes in cognitive demand affect pupil dilation, which is a well established physiological marker of cognitive effort and workload [180, 252, 253].

We hypothesize that as the cognitive demands increase, as evidenced by higher cognitive load (e.g. working memory load) requirements, participants will exhibit greater pupil dilation. Dilation reflects the heightened cognitive load associated

with the instantiation and maintenance of more complex cognitive mechanism. In other words, we anticipate that tasks requiring participants to retain and manipulate multiple line orientations simultaneously will evoke larger pupil dilation compared to tasks with lower working memory load demands. Our study also hypothesizes that pupil dilation will exhibit distinct patterns between the beginning of task episodes and later stages, reflecting variations in cognitive load across different phases of task execution, which arises from different task difficulty conditions. This hypothesis is grounded in the notion that cognitive load is not a unitary construct but rather comprises various components that may variate over the course of task engagement.

By systematically manipulating working memory load within extended task paradigms, our study aims to provide valuable insights into the relationship between cognitive load and pupil responses [254, 255, 256]. Understanding how pupil diameter varies in response to changes in task complexity can offer important implications for assessing cognitive load in real world settings and informing the design of interventions aimed at optimizing cognitive performance and mental workload management. In the investigation of the influence of cognitive load on psychophysiological responses, such as pupil diameter, participants were engaged in a study involving two types of extended tasks varying in overall complexity. At the outset, participants were instructed to memorize the orientations of either one or two lines, denoted as task B lines. This information was to be held in working memory as they proceeded to perform a distinct task, namely task A. Task A involved the encoding and subsequent recall of line orientations. Following the completion of task A, participants were prompted to recall the orientation of one of the task B lines they had initially memorized.

2.2 Methods

The primary objective of this study was to examine the impact of working memory load on the retention and recall of line orientations. Participants were tasked with holding specific line orientations in their working memory and subsequently

recalling a probed line orientation. The experiment comprised two distinct tasks: task A necessitated immediate recall, while task B involved the retention of line orientations for a brief duration before recall.

Experiment started with presentation of task B lines (step 1). The manipulation of working memory load was facilitated through two conditions: a low cognitive load (easy) condition and a high cognitive load (difficult) condition. In the low cognitive load (easy) condition, participants were presented with one line from task B, whereas in the high cognitive load (difficult) condition, two lines from task B were presented. Each trial commenced with the display of one or two lines from task B, contingent upon the assigned load condition. Participants pressed a key when they decided that they memorized line or lines from task B. Two lines from task A (step 2) were presented following task B presentation, participants were again pressed a key when they decided that they memorized two lines from task A. After task B and task A presentation, a mask was presented for 500 ms. On the recall part, firstly, one line (randomly selected) from task A were given with a different orientation (cue) and participants were asked to rotate the cue to its original orientation (recall) by pressing the given keys (step 3). After participants recalled lines from task A, they were asked to recall one given line from task B as they did for task A (step 4). On the low cognitive load (easy) condition, participants cued and recalled the only line that was given on the presentation part of task B, on the high cognitive load (difficult) condition, same as they completed task A, cue was randomly selected from one of the two lines presented on the presentation part of task B.

Throughout two sessions, participants completed a total of 40 easy (low cognitive load) conditions and 40 difficult (high cognitive load) conditions, with each type interleaved with the other. The sequence reset after every set of four conditions; for instance, the first set of four conditions might follow the order easy-difficult-easy-difficult, while the next set could shift to difficult-easy-difficult-easy. Following each recall attempt, participants received feedback delineating the degree of error in reporting the line orientation. For instance, if the correct line orientation had an obliquity of 85 degrees but the participant reported an orientation of 75 degrees, the feedback would indicate an error of 10 degrees.

Experimental procedure was implemented using the Python programming language. Stimuli were delivered in a dark room on a computer monitor (NEC MultiSync LCD 2190UXP monitor, size 21 in, resolution: 1600x1200, refresh rate: 60 Hz), visible to the participants who rested their chins and maintain their position on a chin supporter 57 cm away from the screen. Pupil dilation was recorded throughout the experiment via an Eye Tracker 6 (Applied Science Laboratories, Bedford, MA, USA). We recalibrated the eye tracker for every participant with a standard nine point procedure before the experiment. Participants reported their responses via arrow keys on the keyboard.

A total of 30 participants (20 female, mean age = 20.6, SD = 1.1, age range = 18-23) right handed, with normal or corrected vision took part in the pupil dilation experiment. Participants education level were mostly undergraduate degree (29 undergraduate degree, 1 Ph.D. degree). Prior to participation, they provided written consent, and experimental protocols and procedures were approved by the Research Ethics Committee of Bilkent University, Turkey. All data collection occurred in National Magnetic Resonance Research Center (UMRAM), Bilkent University.

2.3 Results

2.3.1 Behavioral Results

Statistical analysis (Paired Sample T-Test) of behavioral experiment showed differences on response times (RT), easy (low cognitive load) condition was significantly lower than difficult (high cognitive load) condition on task B line presentation (step 1) (Mean easy = 3.76, Mean difficult = 6.18, $t(29)= 7.35$ $p < 0.001$, 95% confidence intervals of difference (CI)= [1.7, 3.1]) and recall (step 4) (Mean easy = 4.34, Mean difficult = 5.22, $t(29)= 6.34$ $p < 0.001$, 95% CI= [0.6, 1.2]) but no difference was presented between task A line presentation (step 2) (Mean easy = 3.93, Mean difficult = 3.75, $t(29)= 1.3$ $p > 0.05$, 95% CI= [-0.4, 0.1]) and

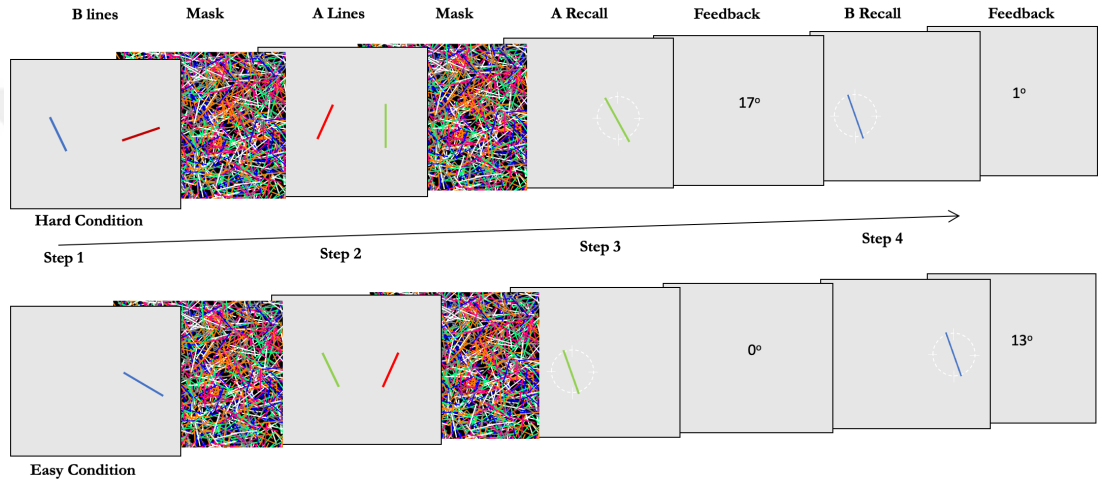

Figure 2.1: Experimental design of line orientation pupil dilation experiment. After the start of the experiment participants saw either 1 line presented (easy conditions) or 2 lines presented (difficult conditions) in B line presentation (step 1) for them to hold in their memory. Remaining of the experiment did not differ between low cognitive load (easy) or high cognitive load (difficult) conditions. Participants saw 2 lines presented for them and held them in their memory at A line presentation (step 2). One of the lines that they had memorized at A line presentation was given to them with different orientation, participants rotated the given cue according to their memory at A line recall (step 3). Then, one of the lines that they had memorized at B line presentation was given to them with different orientation, participants again rotated the given cue according to their memory at B line recall (step 4).

recall (step 3) (Mean easy = 4.07, Mean difficult = 4.02, $t(29)= 0.7$ $p > 0.05$, 95% CI= [-0.2, 0.1]). In terms of recall accuracies, the recall of task A (step 3) (Mean easy = 11.25, Mean difficult = 13.07, $t(29)= 3.1$ $p < 0.005$, 95% CI= [0.6, 3.0]) as well as task B (step 4) (Mean easy = 13.63, Mean difficult = 19.33, $t(29)= 5.6$ $p < 0.05$, 95% CI= [3.6, 7.8]) were both expectedly poorer during difficult (high cognitive load) condition compare to easy (low cognitive load) condition. Furthermore, since participants were instructed to hold task A in their memory for a shorter period of time overall accuracies were better than task B.

Furthermore, a 2 by 2 repeated measures of ANOVA examined the effects of task type (B (step 1) vs A (step 2) and cognitive load or task difficulty (high versus low or difficult versus easy) on response times. The analysis revealed a significant main effect of task type ($F(1,29) = 38.225$, $p < 0.001$). Additionally, a main effect of load was observed ($F(1,29) = 59.266$, $p < 0.001$), indicating that participants spent more time completing tasks with a high cognitive load (difficult) compared to those with a low cognitive load (easy). There was also a significant interaction effect between task type and load ($F(1,29) = 40.599$, $p < 0.001$). This suggests that the impact of cognitive load on response times varied depending on the type of task being performed. Overall, these findings highlight the complex relationship between task demands, cognitive load, and response times, providing valuable insights into the underlying cognitive processes involved in task performance.

Further, a statistical analysis using a 2 by 2 repeated measures ANOVA examined the effects of task type (B (step 1) vs A (step 2) and cognitive load or task difficulty (high versus low or difficult versus easy) on accuracy. This analysis revealed a significant main effect of task type ($F(1,29) = 18.105$, $p < 0.001$), indicating that participants performed less accurately on the tactile task compared to the n-back task. Additionally, a main effect of load was observed ($F(1,29) = 36.462$, $p < 0.001$), suggesting that accuracy decreased as the working memory load increased, regardless of task type. There was also a significant interaction effect between task type and load ($F(1,29) = 12.612$, $p = 0.001$), indicating that the impact of cognitive load on response times varied depending on the type of

task being performed. Overall, these findings underscore the challenges associated with higher cognitive demands, as reflected in decreased accuracy rates, and highlight the distinct performance characteristics observed across different task types and cognitive loads.

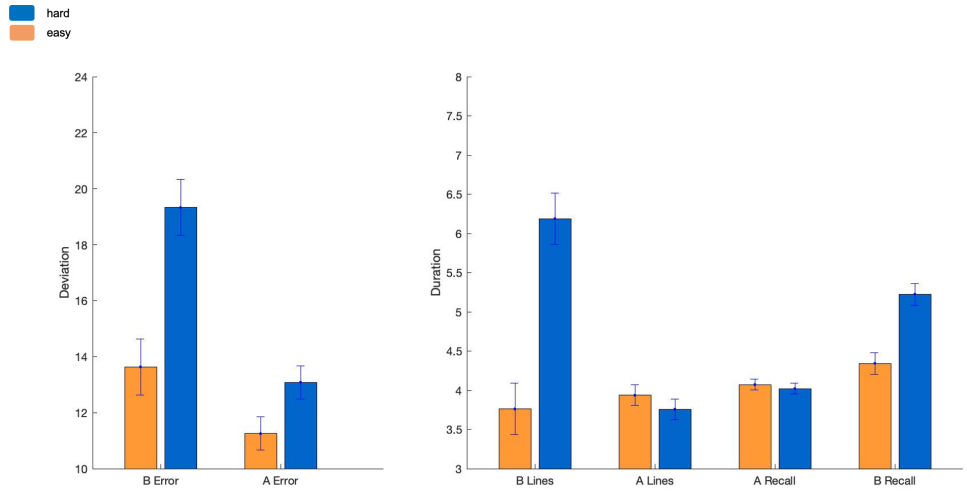

Figure 2.2: Line orientation pupil dilation experiment, deviation from aimed position and response and recall times were shown. recollections were increased error during difficult conditions for both task A and B. They took longer to register line orientations of task B but not task A lines during hard conditions. Recall times were higher only for task B lines and not for task A lines. Error bars represent 95 % confidence intervals.

2.3.2 Pupil Dilation Results

In the pupil dilation experiment, we observed variations in participants' pupil dilation corresponding to different levels of working memory load, which are low cognitive load (easy) condition and high cognitive load (difficult) condition. During the presentation of task B lines (step 1), pupil dilation decreased on the high cognitive load (difficult) condition compared to the low cognitive load (easy) condition. Conversely, during the presentation of task A lines (step 2) pupil dilation

increased on high cognitive load (difficult) condition compared to the low cognitive load (easy) condition. There was no significant main effect. However, there was an interaction effect between task difficulty and type that was statistically significant ($F(1,29) = 12.3$, $p = 0.001$).

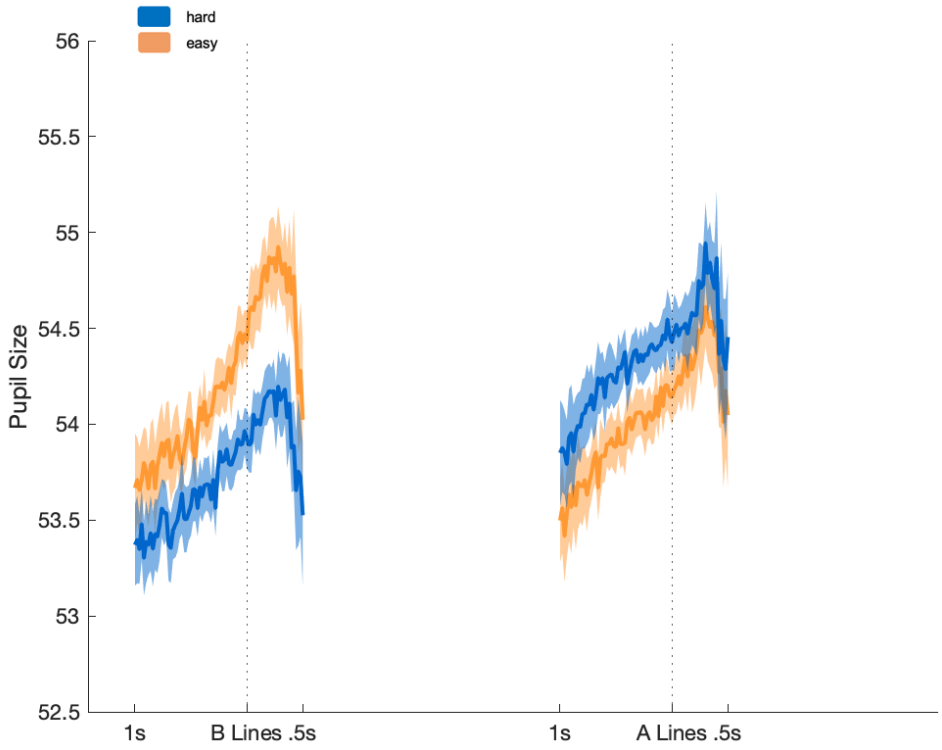

Figure 2.3: A display of time-series graph illustrating changes in pupil size during the first two steps of both the difficult and easy task segments. Use of dotted vertical lines to indicate when participants pressed the button signifying the completion of each step. The plots should depict pupil size 1 second before and 500 milliseconds after each button press.

2.4 Discussion

In our pupil dilation experiment, we meticulously tracked participants' pupil responses to varying levels of cognitive load, characterized by easy (low cognitive load) and difficult (high cognitive load) conditions. Across different stages of the

experiment, including the presentation of task A and task B lines, we observed notable variations in pupil dilation corresponding to the manipulation of working memory load. Specifically, during the presentation of task B lines (step 1), participants exhibited a reduction in pupil dilation on the high cognitive load condition, compared to the low cognitive load condition. This decrease in pupil dilation suggests a physiological response indicating decreased cognitive effort or engagement during the perception of more demanding stimuli [164, 163]. This counterintuitive reduction indicates that at this stage, cognitive effort may not immediately escalate with task difficulty but instead reflect a preparatory or perceptual adjustment phase before active memory encoding begins [257, 258].

Conversely, during the presentation of task A lines (step 2), we observed a contrasting pattern: pupil dilation increased with higher cognitive load (difficult) condition compared to the lower cognitive load (easy) condition. This heightened pupil dilation likely reflects increased cognitive effort or cognitive processing demands required to encode and retain, information under conditions of elevated working memory load [254, 259, 256, 260, 261, 193, 262]. The effect of cognitive load on pupil size differed between the presentation of task B lines (step 1) and task A lines (step 2), indicating distinct responses based on task type and difficulty level. This interaction effect between task difficulty and type (A or B) was statistically significant, underscoring the interactive relationship between cognitive demand and pupil dilation. Our findings offer significant insights into the intricate relationship between cognitive workload and physiological responses, specifically focusing on the role of pupil dilation as a sensitive indicator of cognitive effort. By analyzing pupil dilation across a range of task contexts and difficulty levels, we have been able to highlight how this physiological marker dynamically reflects the brain's adaptation to varying cognitive demands [263, 174].

At its core, pupil dilation is influenced by the activation of the autonomic nervous system [264, 165], and more specifically, it is a reflection of the balance between parasympathetic and sympathetic activity in response to cognitive load [265]. When individuals engage in tasks that are cognitively demanding, the sympathetic branch of the autonomic system becomes more active, leading to an increase in pupil dilation [266]. Our results show a clear distinction in pupil

responses when participants were exposed to tasks of varying difficulty levels, such as low cognitive load versus high cognitive load conditions. In the initial part of tasks which is B lines presentation (step 1) with lower cognitive load (easy conditions), pupil dilation exhibited an increase. Conversely, in the initial part, higher cognitive load (difficult) conditions linked with decreased pupil dilation. interestingly, after the initial part, this trend reversed on the continuation of tasks starting from A lines presentation (step 2). during this period, tasks with lower cognitive load (easy) conditions linked with decreased pupil dilation, suggesting that the brain was not requiring substantial resources to process these tasks. Conversely, during tasks with higher cognitive load (difficult conditions), we observed a marked increase in pupil dilation, indicating that participants were allocating more mental resources and effort to meet the task's challenges. These findings supports the notion that pupil dilation can act as a direct, real-time indicator of cognitive effort, providing a window into the brain's attempt to cope with heightened demands.

The pupil responses pattern revealed by our data based on different phases of task execution hold curious links with cognitive mechanisms[267]. For instance, during the initial presentation of stimuli, pupil dilation may decrease in response to high cognitive load (difficult) conditions but not in response to low cognitive load (easy) conditions, as seen in certain phases of our experiments. This could be attributed to the anticipatory cognitive processes where participants were preparing to engage with the task. However, as tasks progressed and participants became more deeply involved in processing information and working memory, particularly during more challenging conditions, pupil dilation increased significantly [268]. This highlights the adaptive nature of the brain's response, where cognitive effort intensifies as task complexity deepens [153].

The distinct pupil dilation patterns observed in different phases of the task, such as the initial engagement versus the ongoing processing stage, underscore the importance of considering the temporal dynamics of cognitive load. The fact that pupil dilation fluctuated in response to task difficulty not only at the onset but also during the sustained execution of tasks, demonstrates that cognitive workload is not a static phenomenon but rather a continuously evolving process

that unfolds as the brain adapts to different levels of challenge [269].

Overall, these findings provide compelling evidence that pupil dilation serves as a reliable and sensitive biomarker of cognitive demands. The ability of pupil responses to reflect varying degrees of cognitive demand across different task types and contexts suggests that pupillometry can be a valuable tool in studying cognitive processing in real time. Moreover, this research underscores the potential for using pupil dilation as a noninvasive measure to assess cognitive workload in a wide array of settings, from experimental psychology to applied environments such as education, ergonomics, and human-computer interaction. By deepening our understanding of the relationship between cognitive load and physiological responses, we can gain richer insights into the mechanisms underlying cognitive control, mental effort, and performance optimization in both everyday tasks and more complex cognitive challenges. [270, 271, 272].

Chapter 3

Line Orientation fMRI Experiment

3.1 Introduction

Cognitive control plays a critical role in managing heightened cognitive demands, and specific brain regions, known as frontoparietal regions or multiple demand (MD) regions, which are intricately involved in this cognitive process [41, 273, 274, 275]. These regions include the inferior frontal sulcus, anterior insula, intraparietal sulcus, and anterior prefrontal cortex. They exhibit discernible activation patterns in response to increased cognitive demands, particularly when confronted with tasks that necessitate augmented working memory load [14, 218]. These MD regions are instrumental in attentional control and the execution of goal-directed activities across a range of cognitive tasks [276, 219, 277, 20]. Anticipated findings suggest that the more complex task, which necessitates the simultaneous retention of multiple line orientations, will evoke pronounced activation within MD regions in comparison to the simpler task. Such heightened neural activity reflects the augmented cognitive load and the engagement of cognitive control mechanisms requisite for successful execution of the more intricate cognitive mechanism [135].

Moreover, certain cognitive loads experienced during periods of rest elicit deactivation within a distinct set of brain regions known as the default mode network (DMN) [278, 279, 280]. These regions, encompassing the anteromedial prefrontal cortex, posterior cingulate cortex, and temporoparietal junctions, have been linked to various cognitive processes, including stimulus independent thought and mind wandering, which tend to increase when individuals are not actively engaged in specific tasks [73]. Additionally, DMN contribute to scene construction, self projection, future oriented thought, and the recollection of past experiences, further supporting their involvement in mind wandering during rest [226, 227, 281, 77, 84, 282, 283, 284, 285, 286]. However, it should be noted that these regions are not exclusively associated with rest related processes, as they also play a role in task relevant functions such as motor planning [47, 287, 288, 289].

The cognitive load that leads to deactivation in default mode network is determined by the length and complexity of the extended task in which cognition is currently engaged, rather than the complexity of individual component actions [229, 285]. This load does not specifically pertain to the demands of the ongoing action itself, but rather reflects the requirements imposed by the larger task in which the behavior is embedded [229, 285]. Recent research challenges the notion that task-related deactivations occur exclusively within predetermined regions and suggests that such deactivations can manifest in any region not currently engaged in a specific task, contradicting theories proposing an anti correlation between MD regions and DMN [50, 290, 291, 292]. The extent of deactivation in various brain regions, including those within the default mode network, correlates with the difficulty or cognitive load of active programs [50, 293, 122, 294].

Notably, the deactivation observed in brain regions known to deactivate in response to cognitive load tends to be most pronounced at the initiation of extended tasks and gradually diminishes as the task progresses, with activity eventually returning to baseline levels towards the task's conclusion, furthermore, cognitive mechanisms associated with more difficult tasks are anticipated to be larger in scale [50, 295]. Consequently, cognitive mechanism related deactivation within these regions is particularly prominent at the outset of more difficult tasks

[50, 295, 127, 296, 285].

The current study sought to advance our comprehension of how the instantiation of cognitive mechanism impacts functional magnetic resonance imaging (fMRI) activity. As previously elucidated in the pupil dilation experiment, the experimental design encompassed two extended tasks, each with distinct levels of complexity. In the more intricate task, participants were tasked with retaining the orientations of two lines throughout its duration, while the simpler task required the retention of a single line orientation. Extensive empirical evidence supports the notion that additional working memory load engenders heightened activation within MD regions associated with cognitive control, as evidenced by the phenomenon of pupil dilation. Moreover, the investigation aimed to discern disparities in pupil diameter and neural responses specifically at the onset of the more complex extended task. By contrasting the initial stages of the more intricate tasks with those of the simpler tasks, we endeavored to elucidate unique psychophysiological and neural signatures associated with the instantiation of cognitive mechanisms.

Furthermore, through a comprehensive investigation of the relationship between pupil diameter and neural responses at the outset of the more complex task, we aim to unravel the intricate relation between psychophysiological and neural markers of cognitive load. Such an in depth understanding of these disparities and associations has the potential to furnish valuable insights into the underlying cognitive processes that govern the initiation of extended tasks. Moreover, it has the capacity to shed light on the dynamic nature of cognitive control and the efficient allocation of cognitive resources in response to variations in task complexity. In the line orientation fMRI experiment, It is crucial to recognize that certain cognitive mechanisms are instantiated at the beginning of the task episode and linked with deactivation. In essence, one can assume that fMRI activation would be higher on conditions that require high cognitive load (difficult conditions) compare to low cognitive load (easier conditions) [246, 297, 298, 299]. However, in the beginning of the conditions the case should be the opposite if such mechanisms have an impact to BOLD activation.

3.2 Methods

fMRI scans were conducted using a 3-Tesla Siemens MAGNETOM Tim Trio scanner equipped with a 32-channel phased array head coil. The imaging utilized a sequential descending T2*-weighted gradient-echo planar imaging (EPI) acquisition sequence with the following parameters: acquisition time of 2000 ms, echo time of 30 ms, 32 oblique slices with a slice thickness of 3 mm and a 0.75-mm interslice gap, in-plane resolution of 3.0 $\times$ 3.0 mm^2, matrix dimensions of 64 $\times$ 64, a field of view measuring 192 mm, and a flip angle of 78°. T1-weighted MPRAGE structural images were obtained for all participants, featuring a slice thickness of 1.0 mm, resolution of 1.0 $\times$ 1.0 $\times$ 1.0 mm^3 isometric voxels, a field of view spanning 256 mm, and 176 slices. GRAPPA and phase oversampling were applied at 20% with an acceleration factor of 2.

Preprocessing was carried out using Statistical Parametric Mapping (SPM). Functional images underwent slice-time correction using the middle slice as a reference, followed by co-registration with structural T1-weighted images. Subsequently, realignment and normalization to the Montreal Neurological Institute (MNI) template were performed. EPI images were resampled to a resolution of 2 x 2 x 2 mm^3 and then smoothed using an 8-mm full-width at half-maximum Gaussian kernel. The dataset underwent high-pass filtering with a cut-off frequency of 128 seconds.

A similar experimental design that has been used in the line orientation pupil dilation employed on line orientation fMRI experiment. Both easy (low cognitive load) and difficult (high cognitive load) conditions began with a start-screen, which remained until button press, followed by Step 1 (presentation of task B). During this step, lines were displayed around the center, with the two lines presented during difficult conditions always being of different colors. These lines remained visible until participants pressed a button. Immediately after the lines disappeared, a mask screen was presented for 500 milliseconds. This was succeeded by Step 2 (presentation of task A), which also remained until a button press, followed by again a mask screen after its completion. In step 3 (recall of

task A), participants were then prompted to recall one of the line orientations presented in Step 2. The probe indicating the line orientation to be recalled appeared at the identical position and shared the same color as the original line. Participants adjusted the probe orientation by pressing buttons; each press resulted in a 1° change in orientation, either clockwise or anticlockwise. Following adjustment, participants confirmed their response with a separate button press. Feedback indicating the angular deviation between their response and the actual orientation was then provided. In Step 4 (recall of task B), participants recalled the orientation of one of the lines presented in Step 1. Similar to Step 3, the probe was presented in the same color and location as the line to be recalled, and the adjustment process mirrored that of Step 3. Feedback regarding the angular deviation between the participant's response and the original orientation was given afterward. The start-screen for the subsequent condition followed Step 4. Each step had jittered gaps, which ranges from 0.5 to 6 seconds, determined from the offset of the preceding step to the onset of the next.

Participants completed a total of 20 easy and 20 difficult conditions, with each type interleaved with the other. The sequence reset after every set of four conditions; for instance, the first set of four conditions might follow the order easy-difficult-easy-difficult, while the next set could shift to difficult-easy-difficult-easy. Data collection occurred across two separate fMRI runs, with each run comprising 10 easy and 10 difficult conditions and lasting between 15 to 25 minutes. Stimuli were presented on an MR-safe 32-inch LCD Monitor with a refresh rate of 60Hz and spatial resolution of 1600 x 1200 pixels, viewed through a mirror attached to the head coil. Participant responses were recorded using an MR-safe button box. The experiment was conducted using PsychoPy version 2021.2.3 [300].

In order to capture activity associated with each of our events of interest without assuming hemodynamic responses, we modeled 12 seconds of activity following the onset of each of the four steps using six 2-second-long finite-impulse regressors [301]. Steps related to easy and difficult conditions were modeled separately. We then contrasted the activity estimates following steps 1 and 2. We used a difficult>easy contrast to identify regions with higher average activity across the six regressors during steps 1 and 2. Furthermore, we conducted a

repeated-measures of ANOVA to identify regions where the effect of difficulty differed across steps 1 and 2.

To investigate brain regions associated with cognitive control demands, we utilized well-established regions of interest (ROIs) from the MD regions and DMN. Spherical ROIs with a diameter of 10 mm were employed. These included bilateral inferior frontal sulcus (IFS; ± 41 23 29), intraparietal sulcus (IPS; ± 37 -56 41), anterior insula extending into the frontal operculum (AI/FO; ± 35 18 3), and anterior prefrontal cortex (APFC; 27 50 23 and -28 51 15) [16, 302]. DMN ROIs encompassed the posterior cingulate cortex (PCC; -8 -56 26), anteromedial prefrontal cortex (aMPFC; -6 52 -2), and temporoparietal junction (TPJ ± 54 -54 28) [70, 47]. All coordinates are provided in MNI space. The ROIs were generated using the MarsBaR toolbox for SPM, and ROI analyses were conducted using the same toolbox. Statistical analyses were performed using the JASP platform (version 0.16.4).

In this fMRI experiment, 30 participants (20 female) took part, with a mean age of 21.5 (SD = 3.4, age range = 18-34). All participants were right-handed and had normal or corrected vision. The majority have attained undergraduate degrees (28 undergraduate degrees, 1 master's degree, 1 Ph.D. degree). Before participating, they provided written consent, and the experimental protocols and procedures were approved by the Research Ethics Committee of Bilkent University, Turkey. Data collection took place at the National Magnetic Resonance Research Center (UMRAM), Bilkent University.

3.3 Results

3.3.1 Behavioral Results

The statistical analysis, conducted via paired sample t-test, revealed significant differences in response times (RT) between easy (low cognitive load) and difficult (high cognitive load) conditions across various task steps. Specifically, during

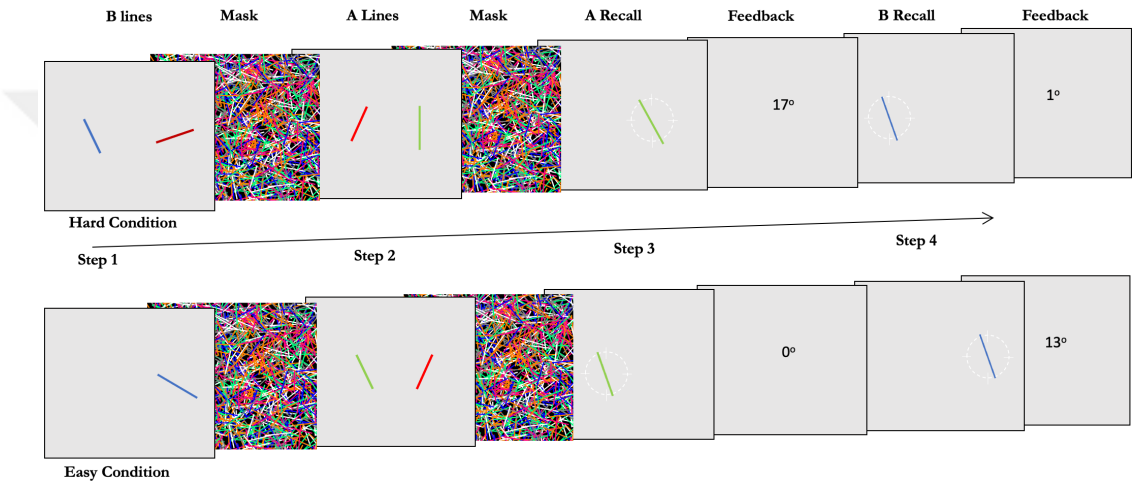

Figure 3.1: Experimental design of line orientation fMRI experiment. After the start of the experiment participants saw either 1 line presented (easy condition) or 2 lines presented (difficult condition) in B line presentation (step 1) for them to hold in their memory. Remaining of the experiment did not differ between low cognitive load (easy) or high cognitive load (difficult) conditions. Participants saw 2 lines presented for them and held them in their memory at A line presentation (step 2). One of the lines that they had memorized at A line presentation was given to them with different orientation, participants rotated the given cue according to their memory at A line recall (step 3). Then, one of the lines that they had memorized at B line presentation was given to them with different orientation, participants again rotated the given cue according to their memory at B line recall (step 4).

task B presentation (step 1), response times were notably shorter in the easy condition compared to the difficult condition (Mean easy = 3.70, Mean difficult = 6.34, $t(29)$=9.69, $p < 0.001$, 95% CI = [2.1, 3.2]). Similarly, during task A presentation (step 2), the easy condition exhibited shorter response times than the difficult condition (Mean easy = 4.97, Mean difficult = 5.60, $t(29)$= 2.40, $p < 0.05$, 95% CI = [0.1, 1.2]). Additionally, during task B recall (step 4), participants responded more quickly in the easy condition compared to the difficult condition (Mean easy = 7.08, Mean difficult = 7.62, $t(29)$=2.86, $p < 0.01$, 95% CI = [0.1, 0.9]). However, no significant differences in response times were observed during task A recall (step 3) (Mean easy = 6.86, Mean difficult = 6.65, $t(29)$=1.1, $p > 0.05$, 95% CI = [-0.6, 0.2]). Regarding recall accuracies, it was anticipated that performance would be poorer under higher cognitive load conditions. This expectation was confirmed during the recall of task A (step 3), where accuracies were lower in the high cognitive load condition compared to the low cognitive load condition (Mean easy = 11.9, Mean difficult = 14.02, $t(29)$= 2.3, $p < 0.05$, 95% CI = [0.3, 3.9]). Similarly, during task B recall (step 4), participants exhibited lower accuracies in the high cognitive load condition compared to the low load condition (Mean easy = 14.80, Mean difficult = 21.60, $t(29)$= 5.3, $p < 0.001$, 95% CI = [4.3, 9.7]). Notably, since participants were instructed to hold task A in memory for a shorter period overall, accuracies were higher compared to task B.

Furthermore, a 2 by 2 repeated measures of ANOVA examined the effects of task type (B (step 1) vs A (step 2) and cognitive load or task difficulty (high versus low or difficult versus easy) on response times. The analysis revealed a no significant main effect of task type ($F(1,29) = 1.952$, $p = 0.173$). However, a main effect of load was observed ($F(1,29) = 59.592$, $p < 0.001$), indicating that participants spent more time completing tasks with a high cognitive load (difficult) compared to those with a low cognitive load (easy). There was also a significant interaction effect between task type and load ($F(1,29) = 30.047$, $p < 0.001$). This suggests that the impact of cognitive load on response times varied depending on the type of task being performed. Overall, these findings highlight the complex relationship between task demands, cognitive load, and response

times, providing valuable insights into the underlying cognitive processes involved in task performance.

Further, a statistical analysis using a 2 by 2 repeated measures ANOVA examined the effects of task type (B (step 1) vs A (step 2) and cognitive load or task difficulty (high versus low or difficult versus easy) on accuracy. This analysis revealed a significant main effect of task type ($F(1,29) = 24.286$, $p < 0.001$) Additionally, a main effect of load was observed ($F(1,29) = 24.483$, $p < 0.001$), suggesting that accuracy decreased as the working memory load increased, regardless of task type. There was also a significant interaction effect between task type and load ($F(1,29) = 7.224$, $p = 0.012$), indicating that the impact of cognitive load on response times varied depending on the type of task being performed. Overall, these findings underscore the challenges associated with higher cognitive demands, as reflected in decreased accuracy rates, and highlight the distinct performance characteristics observed across different task types and cognitive loads.

Statistical analysis (Paired Sample T-Test) for combined results of fMRI and pupil dilation experiments, in terms of response times (RT) revealed that low cognitive load (easy) condition was significantly lower than high cognitive load (difficult) on task B line presentation (step 1) (Mean easy = 3.73, Mean difficult = 6.27, $t(59)= 11.9$ $p < 0.001$, 95% confidence intervals (CI) = [2.1, 3.0]). Low cognitive load (easy) condition was significantly lower than high cognitive load (difficult) condition on task B line recall (step 4) (Mean easy = 5.71, Mean difficult = 6.42, $t(59)= 5.99$ $p < 0.001$, 95% CI = [0.5, 1.0]). No difference was present between task A line presentation (step 2) high cognitive load and low cognitive load (Mean easy = 4.45, Mean difficult = 4.68, $t(59)= 1.46$ $p > 0.05$, 95% CI = [-0.1, 0.5]). No difference was present between task A line recall (step 3) high cognitive load and low cognitive load (Mean easy = 5.46, Mean difficult = 5.33, $t(59)= -1.25$ $p > 0.05$, 95% CI = [-0.3, 0.1]). In terms of recall accuracies, they were expectedly poorer during higher cognitive load condition during the recall of task A (Mean easy = 11.58, Mean difficult = 13.55, $t(59)= 3.7$ $p < 0.001$, 95% CI = [0.9, 3.0]). In terms of recall accuracies, they were expectedly poorer during higher cognitive load condition during the recall of task B (Mean easy = 14.21, Mean difficult = 20.46, $t(59)= 7.7$ $p < 0.001$, 95% CI = [4.7, 8.0])

Furthermore, a 2 by 2 repeated measures of ANOVA examined the effects of task type (B (step 1) vs A (step 2) and cognitive load or task difficulty (high versus low or difficult versus easy) on response times for combined results of fMRI and pupil dilation experiments. The analysis revealed a no significant main effect of task type ($F(1,59) = 3.896$, $p = 0.053$). However, a main effect of load was observed ($F(1,59) = 110.763$, $p < 0.001$), indicating that participants spent more time completing tasks with a high cognitive load (difficult) compared to those with a low cognitive load (easy). There was also a significant interaction effect between task type and load ($F(1,59) = 69.826$, $p < 0.001$). This suggests that the impact of cognitive load on response times varied depending on the type of task being performed. Overall, these findings highlight the complex relationship between task demands, cognitive load, and response times, providing valuable insights into the underlying cognitive processes involved in task performance.

Further, a statistical analysis using a 2 by 2 repeated measures ANOVA examined the effects of task type (B (step 1) vs A (step 2) and cognitive load or task difficulty (high versus low or difficult versus easy) on accuracy for combined results of fMRI and pupil dilation experiments. This analysis revealed a significant main effect of task type ($F(1,59) = 42.731$, $p < 0.001$) Additionally, a main effect of load was observed ($F(1,59) = 54.710$, $p < 0.001$), suggesting that accuracy decreased as the working memory load increased, regardless of task type. There was also a significant interaction effect between task type and load ($F(1,59) = 16.468$, $p < 0.001$), indicating that the impact of cognitive load on response times varied depending on the type of task being performed. Overall, these findings underscore the challenges associated with higher cognitive demands, as reflected in decreased accuracy rates, and highlight the distinct performance characteristics observed across different task types and cognitive loads.

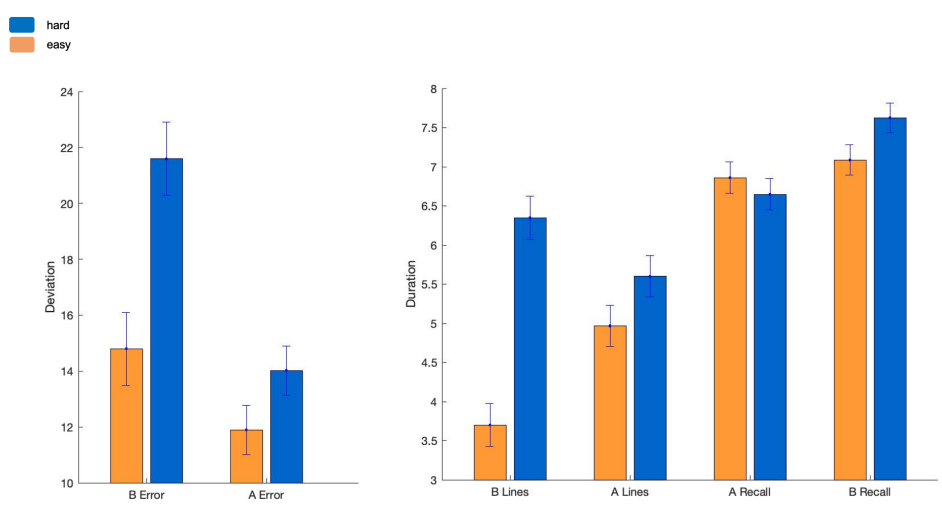

Figure 3.2: The behavioral results from the line orientation fMRI experiment displayed deviations from the aimed position, as well as response and recall times. Notably, during difficult conditions, participants exhibited increased errors in recalling both task A and B line orientations. Additionally, participants took longer to process line orientations in task B, but not in task A, during these challenging conditions. Moreover, recall times were specifically elevated for task B lines, while no significant differences were observed for task A lines. The error bars depicted in the figures represent the 95% confidence intervals.

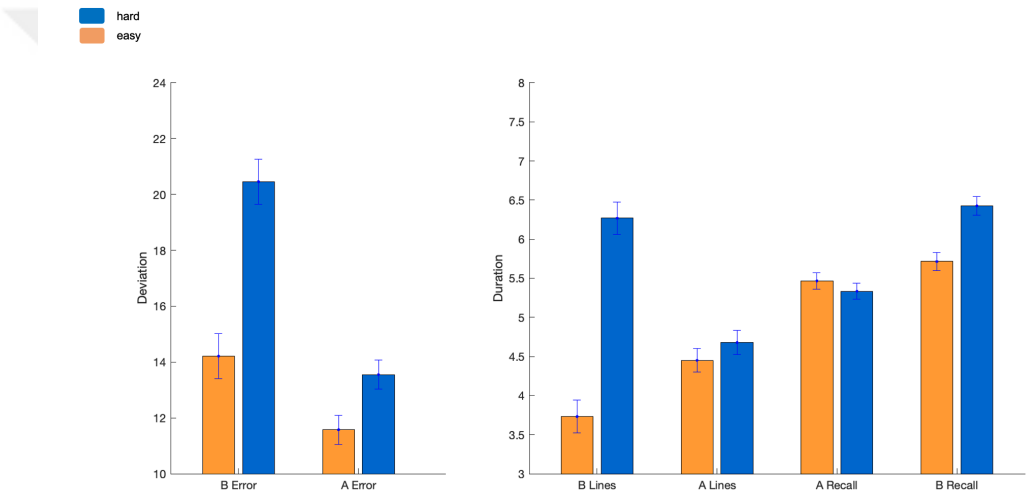

Figure 3.3: The combined behavioral results from the line orientation fMRI experiment and pupil dilation experiment revealed deviations from the aimed position, as well as response and recall times. Notably, during difficult conditions, participants exhibited increased errors in recalling both task A and B line orientations. Additionally, they took longer to process line orientations in task B, but not in task A, during these challenging conditions. Moreover, recall times were specifically higher for task B lines, while no significant differences were observed for task A lines. The error bars depicted in the figures represent the 95% confidence intervals.

3.3.2 fMRI Results

Second level analysis comparing difficult > easy contrast between steps showed imcreased activation patterns represented by hot colors indicating increased activity at step 2 (task A presentation) and decreased activation patterns depicted by cold colors indicating decreased activity at step 1 (task B line presentation) (figure: 3.5). A whole-brain analysis of variance (ANOVA) was performed to assess the effects of difficulty at step 1 (task B line presentation) and step 2 (task A presentation) on neural activation as well. On the whole-brain activation maps, hot colored regions indicated where the effect of difficulty significantly differed between the step 1 (task B line presentation) and step 2 (task A presentation) (figure:3.4). In step 1 (task B line presentation), the difficult condition associated with lower activation compared to the easy condition across several brain regions. Conversely, during the step 2 (task A presentation), the pattern reversed: the difficult condition elicited higher activation than the easy condition. This shift in activation is evident in key regions involved in cognitive control and task management.

ROI analysis show activity time-series during step 1 (task B line presentation) and step 2 (task A presentation) of easy and difficult conditions (figure: 3.4). In numerous MD and DMN regions, activation levels were lower during difficult conditions compared to easy ones at step 1 (task B line presentation). Conversely, at step 2 (task A presentation), activation increased during difficult conditions. This discrepancy in the impact of difficulty between step 1 (task B line presentation) and step 2 (task A presentation) was evident across widespread brain regions, encompassing both MD and DMN regions (table: 3.1).

Our findings revealed that MD regions exhibited greater activation during the difficult conditions, indicating their heightened involvement in processing increased cognitive demands. However, this heightened activation was not observed during step 1 (Task B line presentation). In fact, during step 1, MD regions, as well as other brain regions, demonstrated a decrease in activity compared to the

beginning of easy conditions. This contrasting pattern suggests a dynamic modulation of neural activity in MD regions in response to task difficulty. Although MD regions ultimately show increased activation during step 2 (Task A line presentation) under difficult conditions, their response during step 1 is characterized by decreased activity. This interplay underscores the complex adaptive mechanisms underlying cognitive processing in tasks with varying cognitive demands. Since analyses showed similar activation patterns to line orientation pupil dilation experiment results, these consisted activation patterns between both line orientation experiments suggest a common mechanism of engagement and adaptation to challenging cognitive demands.

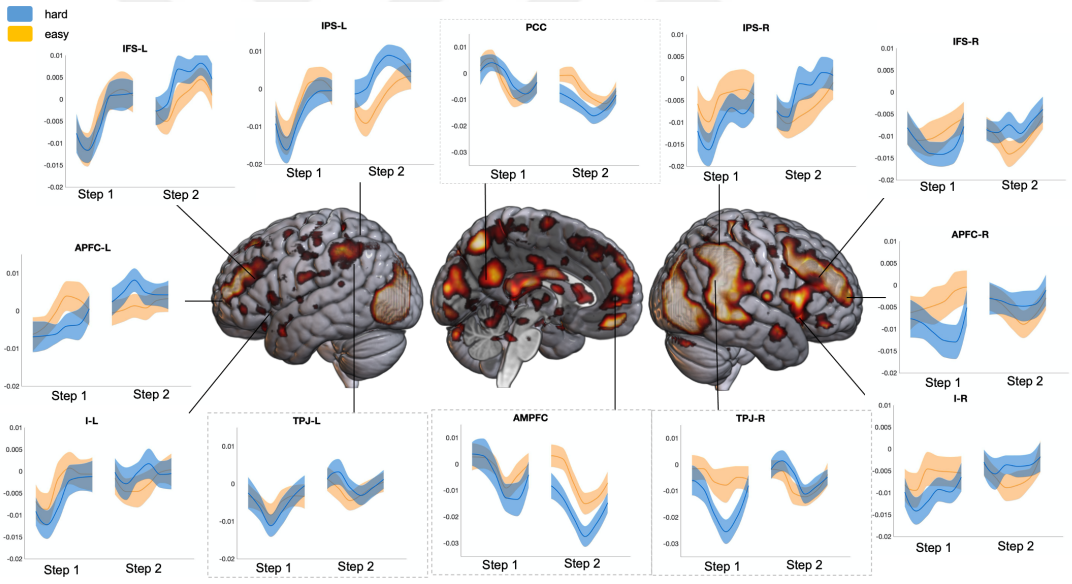

Figure 3.4: The comprehensive brain render ANOVA reveals regions where the impact of difficulty varied notably between steps 1 and 2 (FDR, $p < 0.05$). ROI plots illustrate the temporal activity profiles spanning 12 seconds following the onset of these steps. Across all MD regions, step 1 of the challenging task prompted reduced activity, while step 2 triggered heightened activity compared to their counterparts in the easier task conditions ($F(1,29) > 4.3$, $p < 0.05$ for nearly all depicted ROIs).

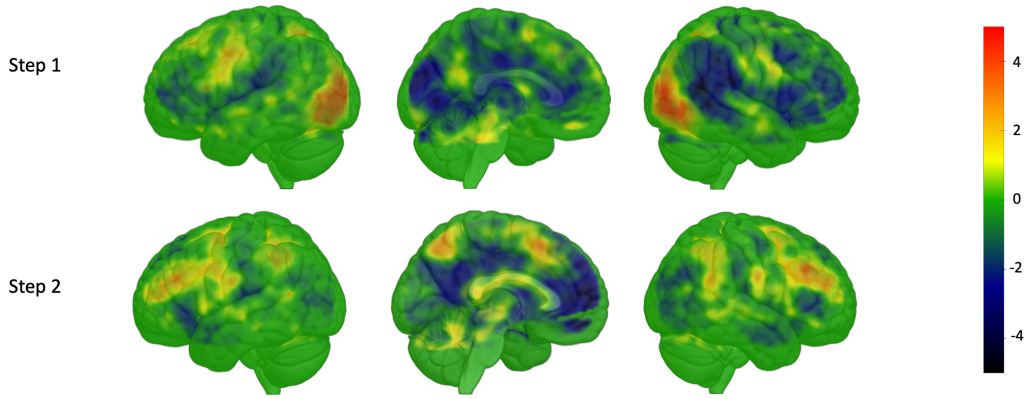

Figure 3.5: The t-maps depicting the contrast between difficult > easy conditions reveal that MD regions exhibited increased activation exclusively during the difficult conditions (main task) (t thresholds corresponding to an FDR correction at $p < 0.01$ is at 3.4), but not at their initiation. Specifically, at the onset of difficult conditions (beginning) (t thresholds corresponding an FDR correction at $p < 0.05$ is at 3.2), MD regions, along with other brain regions, demonstrated decreased activity compared to the beginnings of easy conditions. This suggests a distinct pattern of activation dynamics between difficult and easy conditions, with MD regions showing heightened activity during the challenging phases of the task, but reduced activity at the start of these conditions.

LINE ORIENTATION								
	difficulty		**step**		**difficulty x step**		**difficulty x step x time**	
	df 1,29		**df** 1,29		**df** 1,29		**df** 5,145	
ROI name	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***
TPJ right	5.64	0.02	2.83	0.1	14.2	0.0007	4.8	0.0004
TPJ left	0.1	0.75	6.64	0.02	0.69	0.41	1.72	0.13
AMPFC	7.43	0.01	13.6	0.0009	6.11	0.02	1.26	0.29
PCC	1.81	0.19	12.9	0.001	5.22	0.03	1.96	0.09
APFC right	2.38	0.13	1.01	0.32	5.31	0.03	3.22	0.009
APFC left	0.01	0.91	8.29	0.007	3.08	0.09	1.82	0.11
IFS right	0.002	0.96	0.55	0.47	4.26	0.05	2.82	0.02
IFS left	4.33	0.05	2.75	0.11	2.63	0.12	2.63	0.12
IPS right	0.08	0.78	1.39	0.25	4.77	0.04	1.36	0.24
IPS left	1.04	0.32	10.8	0.003	6.9	0.01	3.23	0.008
AI right	0.27	0.61	4.82	0.04	4.82	0.04	2.58	0.03
AI left	0.11	0.74	2.93	0.1	5.58	0.03	2.34	0.04

Table 3.1: Line orientation experiment fMRI results for repeated measures of ANOVA. Region of Interest (ROI) names are bilateral inferior frontal sulcus (IFS), bilateral intraparietal sulcus (IPS), bilateral anterior insula extending in the frontal operculum (AI), bilateral anterior pre-frontal cortex (APFC), posterior cingulate cortex (PCC) and anteromedial pre-frontal cortex (AMPFC), bilateral temporoparietal junction (TPJ).

3.4 Discussion

Our investigation into the neural dynamics within MD regions and DMN revealed distinct patterns of activity that provide insights into how the brain responds to varying levels of cognitive challenge. At the onset of difficult conditions, we observed lower activation levels in MD regions compared to easy conditions, suggesting that the brain's initial processing of task difficulty involves an early modulation of neural resources. This reduction in activation may indicate a preparatory phase in which cognitive mechanisms adjust to the expected level of demand before full engagement with the task. The brain may initially suppress activity in certain control regions to optimize resource allocation, preventing excessive cognitive effort before task demands are fully established [303].

However, as participants continued to engage in these conditions, a contrasting trend emerged, the sustained neural activity in MD regions increased during the ongoing execution of difficult conditions compared to easy ones. This shift in neural activity dynamics indicates a dynamic adaptation of the brain's response strategy over time [304, 305, 306], with heightened neural engagement observed during the sustained execution of challenging tasks. This heightened activity likely reflects increased cognitive effort and resource allocation to maintain performance levels as the task demands persist, which contradicts with the idea of cognitive load as a unitary construct [153].

The difference in neural activity at various stages of task execution; specifically, the disparity between activation at the beginning of a task episode and during sustained task engagement was consistently observed across nearly all MD regions. This finding highlights the complex and dynamic nature of neural responses to cognitive demand. While the initial reduction in activation may represent a cost-efficient allocation of resources, the subsequent increase in sustained activation indicates that maintaining performance under high cognitive load conditions necessitates greater cognitive effort [217, 307]. This adaptation likely reflects an ongoing recalibration of cognitive control mechanisms, where the brain continuously adjusts its level of engagement to balance efficiency with task demands.

The increased neural activity observed in MD regions during the later execution of difficult conditions further supports the brain's adaptive response, executive control and effortful processing to sustained cognitive demands [18, 14]. Early in a task episode, the brain may reduce activation as a strategic approach to conserve resources. However, as the task episode progresses and cognitive demands remain high, the brain appears to recruit additional resources, leading to higher activation in regions responsible for managing complex cognitive processes [308]. This shift in sustained neural activity reveals the brain's capacity to adjust its response in real-time, scaling cognitive engagement in accordance with the difficulty and duration of the task at hand [309].

This phenomenon is particularly noteworthy in light of the broader understanding of cognitive resource allocation. The initial reduction in neural activation may be indicative of a cognitive strategy aimed at maximizing efficiency [310]. When participants first encounter a complex task, the brain may prioritize efficient resource distribution, reflecting an adaptive mechanism to prevent cognitive overload. However, as the task continues and demands persist, the brain's engagement increases, suggesting that more resources are required to maintain performance on difficult tasks. This shift highlights the flexibility and resilience of the MD regions in responding to ongoing cognitive challenges [311].

Additionally, these findings provide further evidence that cognitive effort is not uniformly distributed across a task episode. Instead, it is a continuously changing process that reflects the changing demands of task engagement. Early in a task episode, the brain may prioritize attentional and preparatory processes, whereas later stages require sustained working memory, executive control, and problem-solving mechanisms [312]. This adaptive engagement model challenges the traditional assumption that cognitive effort remains constant throughout a task and instead highlights the need for a temporal perspective when examining cognitive load and neural activation patterns [313].

Importantly, the role of the DMN in these processes also warrants consideration. While traditionally viewed as a network involved in internally-directed thought, DMN has been shown to exhibit task-related deactivation during externally-focused cognitive tasks [69]. Our results suggest that this deactivation is most pronounced at the beginning of difficult conditions on certain regions (e.g., TPJ) included in DMN, potentially reflecting a suppression of mind-wandering and self-referential processing to allow for full engagement with the task, which is very similar to MD regions activation trend in same task episode beginnings [127, 314]. As tasks continue, the degree of deactivation decreases, indicating that the interaction between MD regions and the DMN is more prominent than previously assumed [315]. This dynamic relation between task-positive and task-negative networks further supports the notion that cognitive engagement is not a singular process but rather a coordinated effort that adapts over time.

In summary, our findings provide valuable insights into the temporal dynamics of neural engagement within MD regions and DMN, revealing a complex relation between initial task-related modulation and sustained cognitive effort. The observed shift from reduced activation at task onset to increased engagement during execution suggests that cognitive load is not a fixed entity but a dynamic construct that changes in response to task demands [210, 316, 317, 229]. By elucidating these adaptive neural responses, our study contributes to a deeper understanding of cognitive flexibility and resource allocation, offering important implications for future research on cognitive load, attention regulation, and executive function.

Chapter 4

Tactile Decision Making and Auditory Working Memory N-Back fMRI Experiments

4.1 Introduction

In the line orientation fMRI experiment, participants engaged in tasks involving the processing of line orientations, with varying levels of difficulty imposed by the task conditions. By analyzing neural activity using fMRI, we observed that the initial response to these task episodes differed depending on the level of difficulty [318, 319, 320]. Specifically, at the onset, when participants encountered difficult task conditions, neural activity in key regions associated with cognitive processing, such as the MD regions, exhibited lower levels of activation compared to easier task conditions [321, 322, 41, 15, 41]. This initial reduction in neural activity suggests a characteristic response to the heightened cognitive demands posed by difficult tasks, reflecting an initial adjustment or preparation process as participants engage with the task.

However, as participants progressed through the task episodes and continued

to engage with the tasks, we observed a shift in neural activity patterns. Particularly, during the execution of task episodes, MD regions demonstrated increased activation levels in response to difficult task conditions compared to easier ones. This sustained elevation in neural activity suggests a heightened engagement of cognitive resources as participants grapple with the challenges posed by the task. The observed patterns of neural activity at the beginning and during the task episode course highlight the dynamic nature of cognitive processing and its modulation in response to varying levels of task difficulty.

These findings from the line orientation fMRI experiment are further supported and complemented by results from the line orientation pupil dilation experiments. The pupil dilation experiments provide a psychophysiological perspective on cognitive demand, offering insights into how changes in pupil size correspond to variations in task difficulty. Consistent with the fMRI findings, the pupil dilation experiments revealed distinct patterns of pupil dilation in response to different levels of task difficulty, with fluctuations observed across the course of task execution.

The convergence of findings from both the line orientation fMRI and pupil dilation experiments underscores the multifaceted nature of cognitive demand and its representation in neural and physiological processes. By elucidating the interplay between neural activity and pupil responses across different stages of task performance and difficulty conditions, our study provides a comprehensive understanding of the cognitive processes underlying task engagement and adaptation.

However, the experimental design of both the line orientation fMRI and pupil dilation experiments shared commonalities, particularly in the task paradigm involving the manipulation of line orientations based on participants' visual memory. Meanwhile, these experiments provided valuable insights into the neural and physiological correlates of cognitive demand [323, 324, 134], they focused primarily on a specific aspect of task difficulty.

To further explore the effects of cognitive mechanisms within extended tasks

and their variations across multiple difficulty conditions, we designed two additional fMRI experiments. These experiments aimed to delve deeper into the underlying cognitive processes involved in task execution under varying levels of difficulty.

In the newly designed fMRI experiments, we introduced novel task paradigms that incorporated a broader range of cognitive demands and difficulty conditions. By expanding the scope of task parameters and difficulty levels, we aimed to capture a more comprehensive understanding of how cognitive mechanisms operate within extended tasks.

These additional experiments allowed us to systematically manipulate and investigate various aspects of cognitive processing, such as working memory load, executive control, and attentional allocation [325, 326, 327, 328, 329, 31, 330], across different task conditions. By employing a multidimensional approach to task difficulty, we sought to uncover the intricate interactions between cognitive processes and their neural underpinnings. Overall, the inclusion of these two new fMRI experiments enabled us to conduct a more comprehensive exploration of cognitive mechanisms within extended tasks. By extending our investigation to encompass a wider range of difficulty conditions, we aimed to elucidate the complex relation between cognitive demands, neural activity, and task performance in a sophisticated manner.

The first experiment, the tactile decision making experiment, engaged participants in determining the size of various shapes using their sense of touch. This task required participants to rely on haptic sensations to make judgments about the physical attributes of the shapes presented to them. By focusing on tactile perception, this experiment provided valuable insights into how the brain processes sensory information from the hands and integrates it with cognitive decision making processes.

In contrast, the second experiment, the auditory n-back working memory experiment, tasked participants with completing n-back tasks using auditory stimuli. In this task, participants had to listen to a series of auditory stimuli and

indicate whether each stimulus matched the one presented "n" steps back in the sequence. This task tapped into working memory processes, requiring participants to hold and manipulate auditory information in their minds while performing the task. By examining auditory working memory, this experiment offered a unique perspective on how the brain processes and retains auditory information in the context of cognitive tasks.

By conducting these two experiments, we were able to explore the effects of different sensory modalities (tactile and auditory) on neural activity and cognitive responses. The inclusion of tasks that engaged different sensory systems allowed us to examine how neural activity in key regions, such as the MD regions and DMN, varied across modalities. This comparative approach shed light on the sensory-specific processing mechanisms underlying cognitive tasks and provided insights into the flexibility and adaptability of neural networks in response to different types of sensory input.

Furthermore, by investigating the neural correlates of cognitive tasks across different sensory modalities, we gained a more comprehensive understanding of the brain's functional organization and its role in supporting diverse cognitive functions. This approach not only deepened our understanding of the neural mechanisms underlying tactile and auditory processing but also highlighted the interconnectedness of sensory and cognitive systems in shaping behavior and cognition.

As we observed in the line orientation fMRI experiment, we expect MD and other regions to show various activity patterns on onset of extended tasks and during extended task course based on existing difficulty conditions. At the beginning of task episodes, this deactivation suggests a suppression or downregulation of activity in regions associated with internally focused cognitive processes, such as mind wandering or self referential thinking [224, 72, 331, 228, 332, 333, 334, 335, 336, 337]. This suppression may serve to facilitate the allocation of resources to task-relevant processes and optimize performance on the upcoming task.

The presence of this task-related deactivation at the beginning of task episodes,

particularly in the context of tasks with high cognitive load, highlights the importance of considering the role of cognitive mechanisms in shaping neural activity. Despite the expectation of increased activation in regions associated with high cognitive demand [44, 249, 41], the observed deactivation suggests an interactive relation between MD regions and DMN.

Moreover, such consistency of this activation and deactivation pattern across various fMRI experiments involving different types of tasks that operate underscores its robustness and generalizability. Regardless of the specific cognitive task or sensory modality involved, the brain appears to exhibit a similar pattern of task-related deactivation at the onset of task episodes. Results of these two fMRI experiments have the potential to illuminate a fundamental mechanism by which the brain prepares for and adapts to task demands, highlighting the dynamic nature of cognitive processing and its neural underpinnings.

4.2 Methods

fMRI scans were conducted using a 3-Tesla Siemens MAGNETOM Tim Trio scanner equipped with a 12-channel phased array head coil. The imaging protocol involved a sequential descending T2*-weighted gradient-echo planar imaging (EPI) sequence, featuring an acquisition time of 2000 ms, echo time of 30 ms, 32 oblique slices with a slice thickness of 3 mm and a 0.75-mm interslice gap, in-plane resolution of 3.0×3.0 mm^2, matrix dimensions of 64×64, a field of view measuring 192 mm, and a flip angle of 78°. Additionally, T1-weighted MPRAGE structural images were acquired for all participants, with a slice thickness of 1.0 mm, resolution of $1.0 \times 1.0 \times 1.0$ mm^3 isometric voxels, and a field of view spanning 256 mm, comprising 176 slices.

Preprocessing was performed using Statistical Parametric Mapping (SPM). Functional images underwent slice-time correction using the middle slice as a reference, followed by co-registration with the structural T1-weighted images.

Subsequently, realignment and normalization to the Montreal Neurological Institute (MNI) template were conducted using the DARTEL toolbox. EPI images were resampled to a resolution of 2 x 2 x 2 mm^3 and then smoothed using an 8-mm full-width at half-maximum Gaussian kernel. The dataset was subjected to high-pass filtering with a cut-off frequency of 128 seconds.

The experimental design included two extended tasks: the tactile decision making experiment and the auditory working memory n-back experiment each consists 10 blocks. These extended tasks featured interleaved sequences of easy and difficult blocks. The sequence reset after every set of two blocks for tactile decision making experiment; for instance, the first set of two blocks might follow the order easy-difficult, while the next set could shift to difficult-easy, Each block consisted of 5 easy or 5 difficult trials. For the auditory working memory n-back experiment; for instance, the first block was randomly determined as difficult or easy. Based on the starting block, the sequence followed the direction of difficult-easy-difficult-easy-difficult-easy-difficult-easy-difficult-easy or easy-difficult-easy-difficult-easy-difficult-easy-difficult-easy-difficult, each block consisted 10 easy or 10 difficult trials.

In the tactile decision experimental task, participants encountered a variety of geometric shapes, such as circles, squares, and rectangles, affixed to plexiglas tablets. These tablets were divided into two distinct horizantal categories labeled as easy and difficult blocks, each consisting of 5 trials. Within each trial, participants were presented with a pair of geometric shapes, one of which was consistently larger than the other. The task's complexity was manipulated through two key strategies: adjusting the size difference between shapes and employing embossment techniques to alter the shapes' sensibility on the plexiglass tablets. In easy conditions, the size difference between shapes ranged from 0.8 to 1 cm^2 and embossment level determined as 7 units, while in difficult conditions, size difference narrowed to ranged from 0.3 to 0.5 cm^2 and embossment level decreased to 3 units. The shapes were positioned between vertical lines, each 3 cm wide. Participants' task involved tactile discrimination, requiring them to determine and indicate, using a button box, which of the two shapes was the larger of the pair.

During the fMRI session, an experimenter replaced the tablet every two conditions, positioning them either on the participants' chest or abdomen to ensure optimal comfort and stability. Prescan training involved familiarizing participants with four tablets, while the actual scanning phase utilized a set of ten distinct tablets to ensure variety and prevent habituation effects. Each condition spanned a duration of 15 to 30 seconds, interspersed with brief jittered rest periods of randomized duration ranging from 2 to 10 seconds.

In easy blocks, participants were allowed a longer inter-trial interval of 1.5 seconds to accommodate the simpler task demands. Conversely, in difficult blocks, this interval was reduced to 0.5 seconds to heighten task difficulty and maintain participant engagement. Task instructions were delivered via headphones connected to an auditory stimulus device, providing participants with auditory cues for trial initiation, response execution, and rest intervals. These cues, synchronized with the experimental protocol, ensured consistent timing and facilitated task performance. Participants were encouraged to rest as needed between conditions and signaled the commencement of the next condition by pressing a button.

The experiment was meticulously coordinated using prerecorded auditory instructions delivered through the Psychtoolbox on MATLAB. These instructions guided participants through the experimental protocol, informing them when to begin a trial, when to execute their button press response, and when to rest following the completion of an condition. This standardized approach enhanced experimental control and minimized potential confounds.

The auditory working memory n-back experiment utilized in this study comprised an auditory n-back task, featuring two levels of cognitive demand: a standard 1-back task and a more complex 3-back task, each consisting of ten sequential trials. In both task variations, participants were presented with a series of auditory stimuli composed of Turkish letters.

In the 1-back task, participants were instructed to retain the first letter encountered in their working memory and then determine whether the subsequent trial matched the one immediately preceding them by pressing a designated response

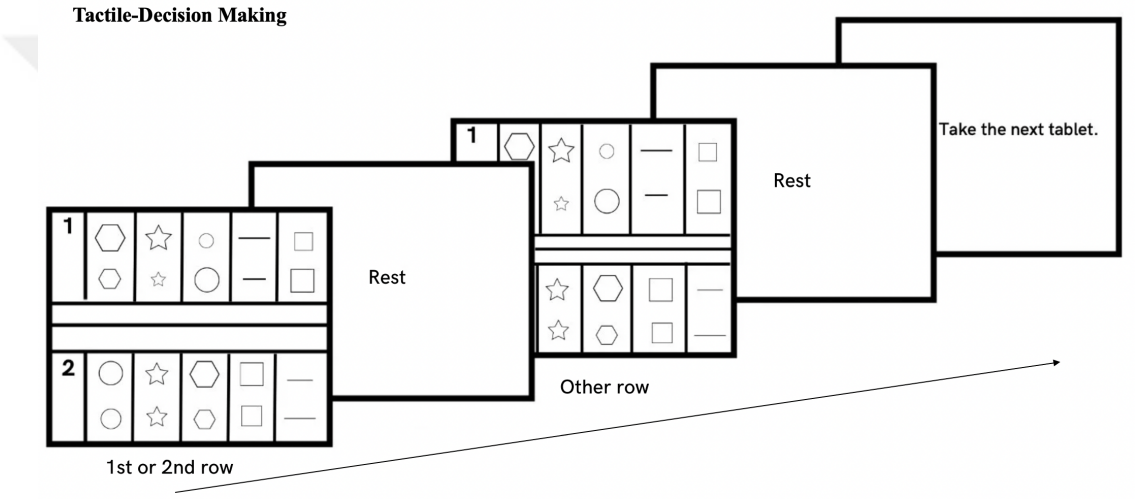

Figure 4.1: The tactile decision-making experiment required participants to determine which of two shapes was larger in the same trial. This tactile discrimination task was conducted using a plexiglass tablet divided into distinct easy and difficult horizantal sections, each comprising 5 trials. Within each trial, participants encountered a pair of shapes drawn with raised margins to facilitate tactile exploration. Notably, the raised margins of shapes on easy trials were more pronounced, enhancing their perceptibility by touch. Additionally, the size discrepancies between shapes within a pair were more substantial in easy trials, providing participants with clearer tactile cues to aid their decision-making process. This carefully designed experimental paradigm aimed to systematically manipulate task difficulty, investigate participants' tactile perception, and decision-making abilities across varying levels of difficulties.

button. This process continued from the second trial onward, with participants progressing through the trial sequence after each response.

The 3-back task followed a similar structure but posed a greater cognitive challenge. Participants initially memorized the auditory sequence of the first three letters encountered and subsequently had to identify whether the current auditory stimulus matched the one heard three letters prior. As with the 1-back task, participants indicated their response via a button press before proceeding to the next trial.

Prior to the actual experiment, participants underwent a 10-minute prescan training session to familiarize themselves with the task requirements. Those who encountered difficulties during prescan training were assigned modified versions of the task, such as a 2-back task (4 individuals) or a 0-back task (1 individual), to ensure that the cognitive demands were appropriate for their skill level.

Following each task block, participants were provided with a brief interlude or rest period, the duration of which varied randomly between 5 to 15 seconds. This randomized interlude aimed to introduce temporal unpredictability into the study design, potentially influencing participants' cognitive processing strategies.

During the scanning procedure, participants were blindfolded to eliminate visual input, allowing them to focus exclusively on tactile and auditory perceptual processing. This methodological choice aimed to isolate the effects of auditory working memory demands on cognitive performance without confounding visual stimuli.

Each task condition was meticulously modeled using three distinct regressors in the General Linear Model (GLM) framework. Firstly, the initiation of each condition was represented as an event with no duration to capture the neural activity triggered by the onset of the condition. Secondly, the entire duration of the condition was modeled as an epoch of the same duration, allowing for the estimation of the average neural activity throughout the condition. Lastly, the conclusion of the condition was modeled as another event with no duration to

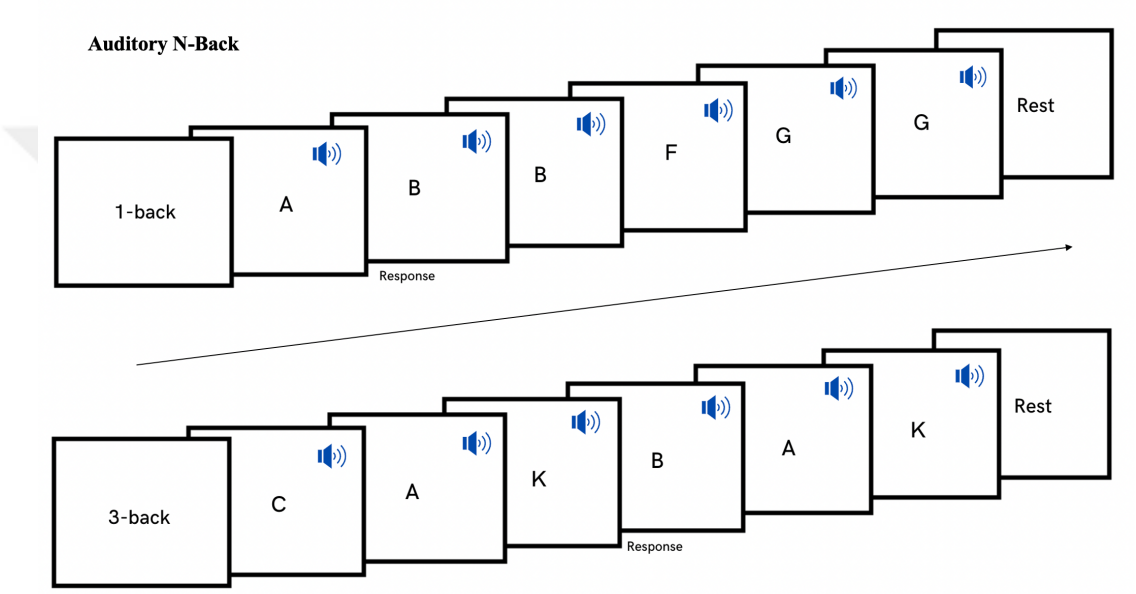

Figure 4.2: The auditory working memory experimental design consisted of a series of blocks, each consisting 10 trials. Participants were tasked with determining whether the auditory letter presented on a given trial matched the one heard either 1 trial back (on easy blocks) or 3 trial back (on difficult blocks). In each condition, participants engaged in a sequence of auditory stimuli, where they were required to maintain and manipulate auditory information in their working memory. This task involved both simple and more challenging cognitive demands, depending on whether participants had to recall the letter from the immediate past or from a more distant past, respectively. By varying the number of trials between the current and target stimuli, the experiment aimed to assess participants' auditory working memory capacity and their ability to process and retain auditory information over short and longer intervals. This design allowed for the investigation of cognitive processes involved in auditory memory retention and retrieval across varying levels of difficulty.

capture the neural activity associated with the termination of the condition.

These modeling approaches were applied separately for both easy and difficult conditions, utilizing different sets of regressors to account for variations in task difficulty. Additionally, movement parameters were incorporated into the GLM as covariates of no interest to control for potential confounding effects of motion. All regressors and covariates were convolved with the standard hemodynamic response function (HRF) to account for the temporal dynamics of the blood oxygen level-dependent (BOLD) signal. These convolved regressors were then entered into the GLM to estimate the neural activity associated with each task condition.

T-contrasts were performed for second level analysis to examine the differences between task phases. The first t-contrast focused on difficult > easy at the beginning of task episode. The second t-contrast focused on difficult > easy during the main task. Furthermore, we conducted a repeated-measures of ANOVA to identify regions where the effect of difficulty differed across the beginning of task episode and during the main task. To explore the neural substrates underlying cognitive control demands, we targeted specific regions of interests (ROIs) known to be implicated in these processes. These ROIs encompassed both the Multiple Demand (MD) regions and Default Mode Network (DMN). We employed spherical ROIs with a diameter of 10 mm to precisely delineate these brain regions. For the MD network, we focused on bilateral regions including the inferior frontal sulcus (IFS; ± 41 23 29), the intraparietal sulcus (IPS; ± 37 -56 41), the anterior insula extending into the frontal operculum (AI/FO; ± 35 18 3), and the anterior prefrontal cortex (APFC; 27 50 23 and -28 51 15). The coordinates for these MD regions were derived from established literature, as reported in studies by Duncan and Dosenbach [16, 302]. These regions are well-established as crucial nodes involved in executive control processes.

In addition to the MD regions, we targeted key nodes of the default mode network, including the posterior cingulate cortex (PCC; -8 -56 26), anteromedial prefrontal cortex (aMPFC; -6 52 -2), and temporoparietal junction (TPJ ± 54 -54 28). The coordinates for these DMN regions were derived from established

literature, as reported in studies by Andrews-Hanna and Vatansever [70, 47]. All coordinates were referenced in Montreal Neurological Institute (MNI) space to ensure consistency across analyses. We utilized the MarsBaR toolbox for SPM to create these ROIs with precision. Subsequent ROI analyses were conducted using the same MarsBaR tool, facilitating robust examination of neural activity within these predefined regions. Furthermore, statistical analyses were performed using the JASP platform (version 0.16.4), enabling comprehensive exploration of the data and robust inference regarding the involvement of these regions in cognitive control demands. This integrated approach ensured meticulous examination of brain activity patterns underlying cognitive control processes, providing valuable insights into the neural mechanisms supporting higher-order cognitive functions.

A cohort of 21 individuals (13 female, 6 left-handed) participated in the fMRI experiment. Their mean age was 27.1 years (SD = 6.2), with ages spanning from 20 to 43 years. The educational background of participants varied, with the majority holding undergraduate degrees (14 participants), while 2 participants had completed high school, 3 held master's degrees, and 2 possessed Ph.D. degrees.

To ensure a controlled experimental environment, participants utilized an eye patch to eliminate any visual input during the experiment. This precaution aimed to minimize potential confounding effects of visual stimuli on neural activation patterns, thus allowing for a more precise investigation of auditory and tactile perceptual processing.

Prior to their involvement, all participants provided written informed consent, demonstrating their voluntary agreement to participate in the study. Furthermore, the experimental protocols and procedures employed were thoroughly reviewed and approved by the Research Ethics Committee of Bilkent University, Turkey. This ethical oversight ensured that the study adhered to established guidelines and safeguarded the rights and well-being of the participants involved.

The data collection procedures took place at the National Magnetic Resonance Research Center (UMRAM) within Bilkent University, a facility equipped with state-of-the-art imaging technology and research infrastructure. This centralized

location provided a controlled and standardized environment for data acquisition, contributing to the reliability and validity of the study findings.

4.3 Results

4.3.1 Behavioral Results

A paired sample T-test revealed significant differences in accuracy levels between easy and difficult conditions for both the tactile decision making experiment ($t(20)= 4.8$, $p <0.001$) and the working memory n-back experiment ($t(20)= 5.4$, $p <0.001$). Participants exhibited higher error rates in the difficult conditions compared to the easy conditions across both experiments, indicating greater difficulty in task performance when cognitive demands were increased.

Furthermore, a statistical analysis using a 2 by 2 repeated measures ANOVA examined the effects of task type (tactile versus n-back) and cognitive load or task difficulty (high versus low or difficult versus easy) on accuracy. This analysis revealed a significant main effect of task type ($F(1,20) = 51.583$, $p < 0.001$), indicating that participants performed less accurately on the tactile task compared to the n-back task. Additionally, a main effect of load was observed ($F(1,20) = 53.785$, $p < 0.001$), suggesting that accuracy decreased as the working memory load increased, regardless of task type.

However, the interaction effect between task type and load was not significant ($F(1,20) = 2.792$, $p = 0.1$), indicating that the influence of load on accuracy did not differ between the tactile and n-back tasks. Overall, these findings underscore the challenges associated with higher cognitive demands, as reflected in decreased accuracy rates, and highlight the distinct performance characteristics observed across different task types and cognitive loads.

The paired sample t-test revealed significant differences in response times between easy and difficult conditions for both the tactile decision making experiment

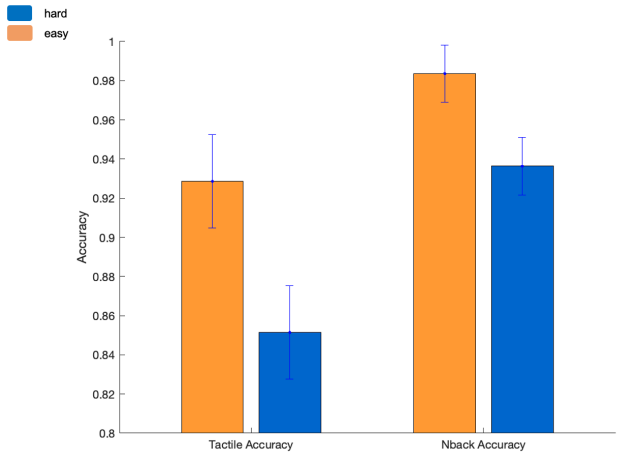

Figure 4.3: In both the tactile decision making experiment and the working memory n-back experiment, participants exhibited significantly higher error rates during the difficult conditions compared to the easy conditions. This suggests that increased cognitive demands associated with the difficult conditions led to more erroneous responses across both experiments. The error bars depicted in the figures represent the 95% confidence intervals, providing insights into the variability and precision of the accuracy measurements. These findings underscore the influence of task difficulty on participants' performance accuracy and highlight the robustness of the observed effects across different experimental paradigms.

($t(20) = 26$, $p < 0.001$) and the working memory n-back experiment ($t(20) = 6.0$, $p < 0.001$). Across both experiments, participants exhibited longer response times during the difficult conditions compared to the easier conditions, indicating that increased task difficulty was associated with slower performance overall.

Furthermore, a 2 by 2 repeated measures of ANOVA examined the effects of task type (tactile versus n-back) and cognitive load or task difficulty (high versus low or difficult versus easy) on response times. The analysis revealed a significant main effect of task type ($F(1,20) = 967.805$, $p < 0.001$), indicating that participants spent more time on the tactile task compared to the n-back task. Additionally, a main effect of load was observed ($F(1,20) = 588.689$, $p < 0.001$), indicating that participants spent more time completing tasks with a high cognitive load (difficult) compared to those with a low cognitive load (easy).

Importantly, there was also a significant interaction effect between task type and load ($F(1,20) = 533.980$, $p < 0.001$). This suggests that the impact of cognitive load on response times varied depending on the type of task being performed. Overall, these findings highlight the complex relationship between task demands, cognitive load, and response times, providing valuable insights into the underlying cognitive processes involved in task performance.

4.3.2 fMRI Results

The second-level analysis for difficult > easy contrast at the outset of task episodes (beginning) and throughout their execution (main task) showed similar activation patterns to line orientation experiments. Hot colors indicated increased activity for task execution (main task) and cold colors indicating decreased activity at the outset of task episodes (beginning). This phenomenon was consistent across both the tactile decision making experiment and the auditory n-back working memory experiment (figure: 4.9), (figure: 4.7), (figure: 4.11). A whole-brain analysis of variance (ANOVA) was performed to assess the effects of difficulty at the initiation (beginning) and execution of tasks (main task) on neural activation as well. On the whole-brain activation maps, hot colored regions indicated where

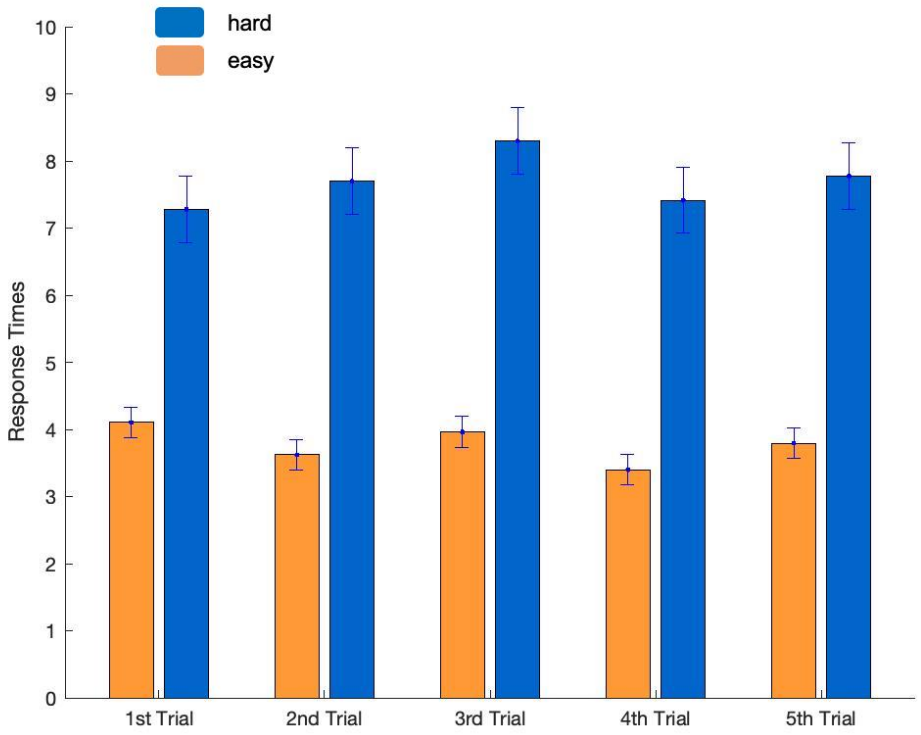

Figure 4.4: In the tactile decision making experiment, participants exhibited prolonged decision-making times when confronted with difficult conditions. Specifically, they required more time to discern and determine which of the presented shapes was larger in size compared to the easier conditions. Error bars indicate 95% confidence intervals. These findings suggest that increased cognitive demands associated with the difficult conditions led to a slower decision-making process, reflecting the participants' efforts to accurately discriminate between the tactile stimuli.

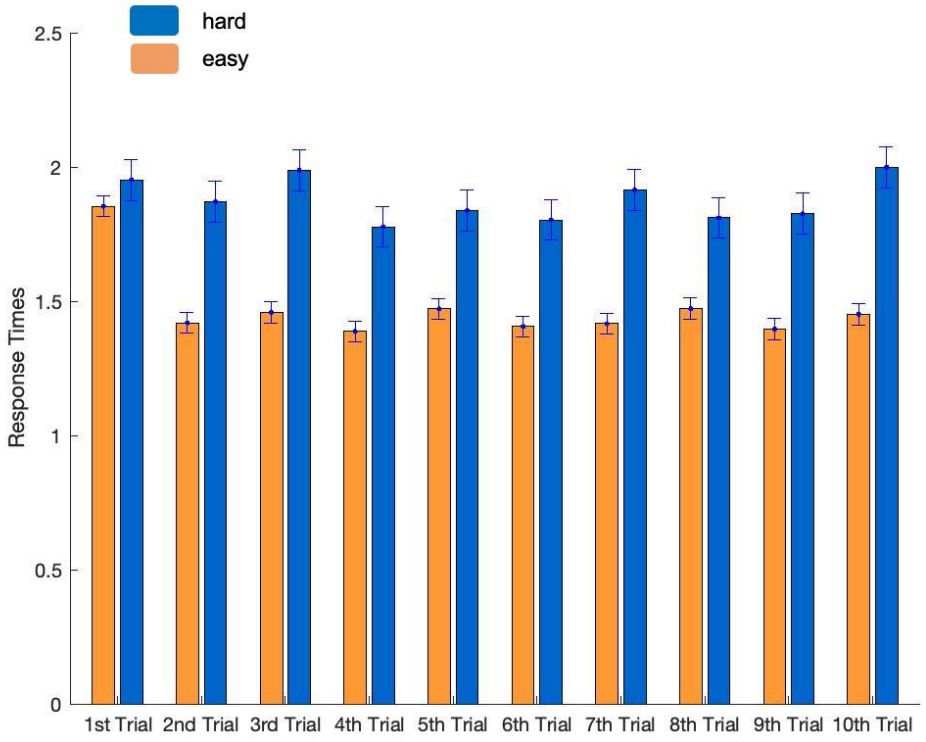

Figure 4.5: In the auditory working memory n-back experiment, participants experienced extended durations in recalling the auditory stimuli from previous trials, particularly during difficult conditions. This observation suggests that participants encountered greater difficulty in retaining and recalling the auditory information presented in the n-back task when cognitive demands were heightened. Error bars indicate 95% confidence intervals. These findings suggest that increased working memory load during the difficult conditions led to prolonged memory retrieval processes, reflecting the participants' efforts to maintain accurate representations of the auditory stimuli over successive trials.

the effect of difficulty significantly differed between the beginning and main task episodes (figure:4.6), (figure:4.8), (figure:4.10).

In terms of ROI's, both experiments consistent activation patterns were observed in regions associated with the MD and certain regions within the DMN across the initiation of the task episode (beginning) and execution phases of the task episode (main task). At the onset of the task episodes, the difficult condition was characterized by decreased activation in the MD regions, while the easy condition exhibited increased activation. However, notably, during the main task execution, the activation pattern reversed, the difficult condition elicited increased activation, whereas the easy condition showed decreased activation nearly on every ROI for MD regions and certain DMN regions (figure:4.6), (figure:4.8), (figure:4.10), (table: 4.2), (table: 4.1), (table: 4.3).

Our findings revealed that MD regions exhibited greater activation specifically during the difficult conditions, indicating their heightened involvement in processing higher cognitive demands. However, this increased activation was not observed during the initial stages of the difficult conditions. Instead, MD regions, along with other brain regions, exhibited a decrease in activity compared to the beginning of easy conditions. This contrasting pattern suggests a dynamic modulation of neural activity in MD regions in response to changes in task difficulty. While they ultimately show increased activation during the execution of difficult conditions, their initial response during the onset of these conditions is characterized by decreased activity. This interplay underscores the complex adaptive mechanisms underlying cognitive processing, particularly in tasks involving cognitive demands. Overall, the similar activation patterns observed at the onset and during the execution of task episodes in both experiments provide compelling evidence of a shared neural response to heightened task difficulty, shedding light on the brain's dynamic processes underlying cognitive processing under challenging conditions.

This reversal in the activation patterns between the beginning and execution phases highlights the dynamic nature of neural responses to task demands. While the initial stages may reflect preparatory processes and allocation of cognitive

resources, the subsequent execution phase involves intensified engagement and allocation of resources to meet the demands of the task. This observed pattern underscores the adaptive nature of neural processing, wherein responses dynamically adjust to match the changing task requirements, ultimately optimizing cognitive performance.

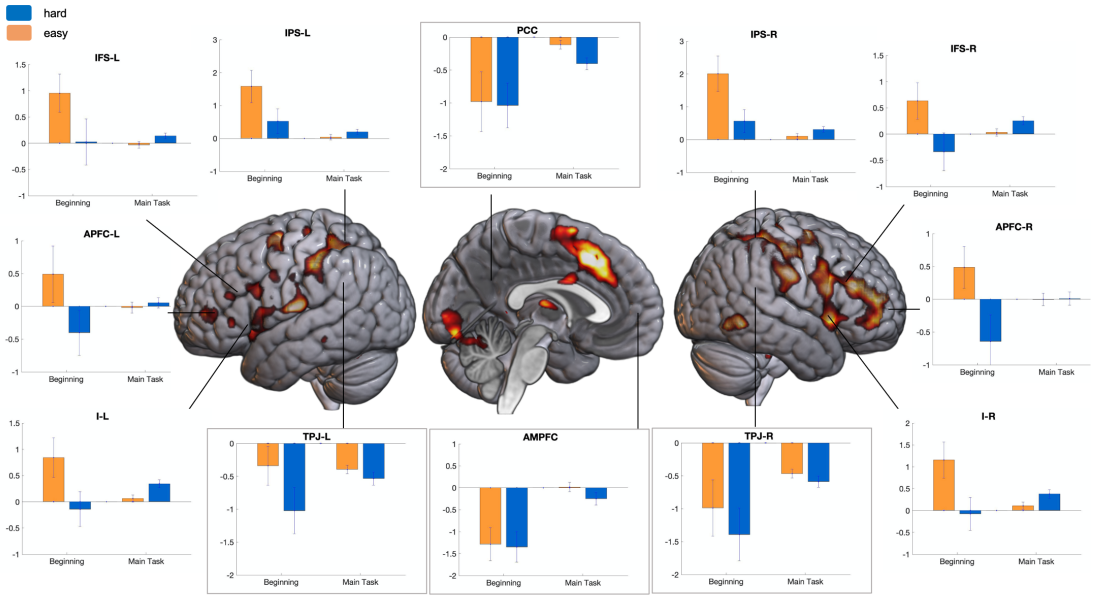

Figure 4.6: Tactile decision making experiment, our whole brain ANOVA provides a visual representation of regions where the impact difficulty differs between the initial phase (beginning) and the subsequent task execution (main task) (FDR, $p < 0.05$). Through ROI plots, we examined the estimates of activity at the beginning and during the task block for both easy and difficult conditions, with error bars representing 95% confidence intervals. In the majority of regions, we observe a distinct pattern: at the onset of difficult conditions, there is a notable decrease in activity compared to the beginning of easy conditions. However, as the task progresses into its main phase, a reversal occurs, particularly evident in the MD regions. Here, difficult conditions exhibit heightened activity levels compared to easy conditions, suggesting a dynamic neural adaptation to the increasing task demands over time.

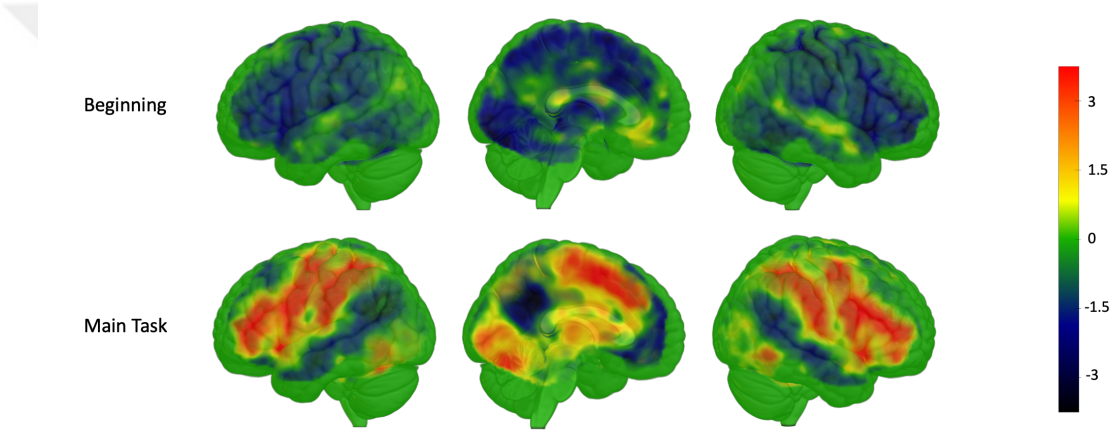

Figure 4.7: Tactile decision making experiment, presented t-maps contrasting difficult > easy at the onset (beginning) of the condition and during its execution (main task). The results revealed that MD regions exhibited increased activation exclusively during the difficult conditions (main task) (t thresholds corresponding to an FDR correction at $p < 0.05$ is at 2.5), but not at their initiation (beginning) (t thresholds corresponding at $p < 0.05$ is at 3.6). Interestingly, at the beginning of difficult conditions, MD regions, along with other brain areas, displayed a decrease in activity compared to the commencement of easy conditions. This pattern suggests a dynamic modulation of neural activity in response to the varying cognitive demands imposed by the task, with MD regions playing a role particularly during the execution phase of challenging conditions.

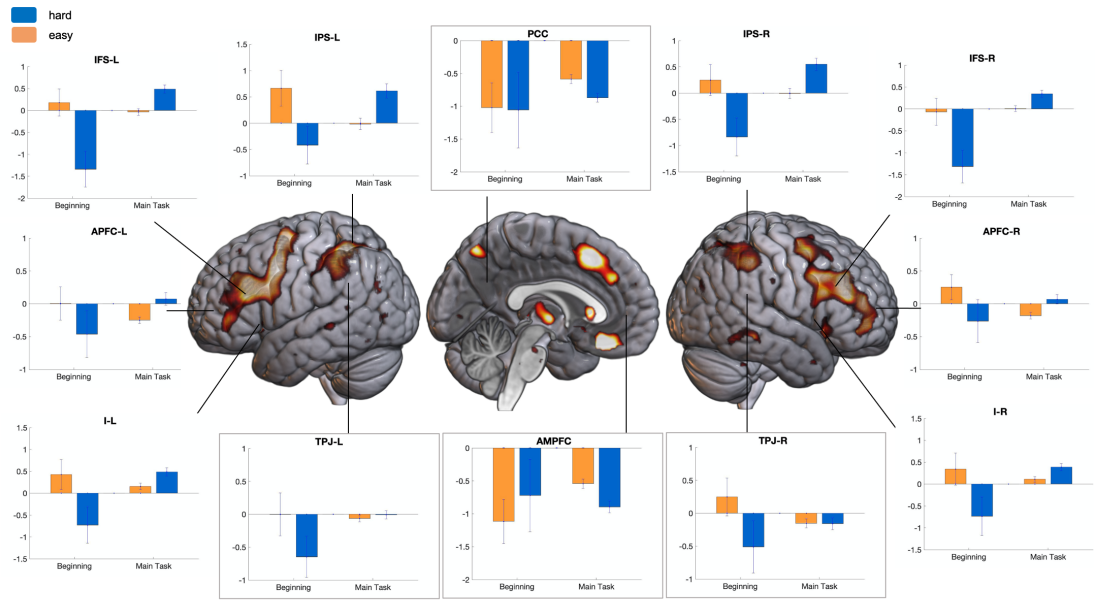

Figure 4.8: Working memory n-back experiment, our whole brain ANOVA analysis revealed brain regions where the impact of difficulty varied between the onset (beginning) and execution phases (main task). Brain render highlighted areas (hot colors) shows where this effect was statistically significant (FDR, $p < 0.05$). ROI plots depicted the estimated activity levels at the beginning and during the main task for both easy and difficult conditions were generated, with error bars representing 95% confidence intervals. Interestingly, in most regions, the initiation of difficult conditions was associated with lower activity compared to the beginning of easy conditions. However, during the main execution phase (main task), this pattern reversed in MD regions. Here, difficult task conditions exhibited higher activity levels compared to their easy counterparts, indicating a shift in neural engagement as the cognitive demands of the task increased.

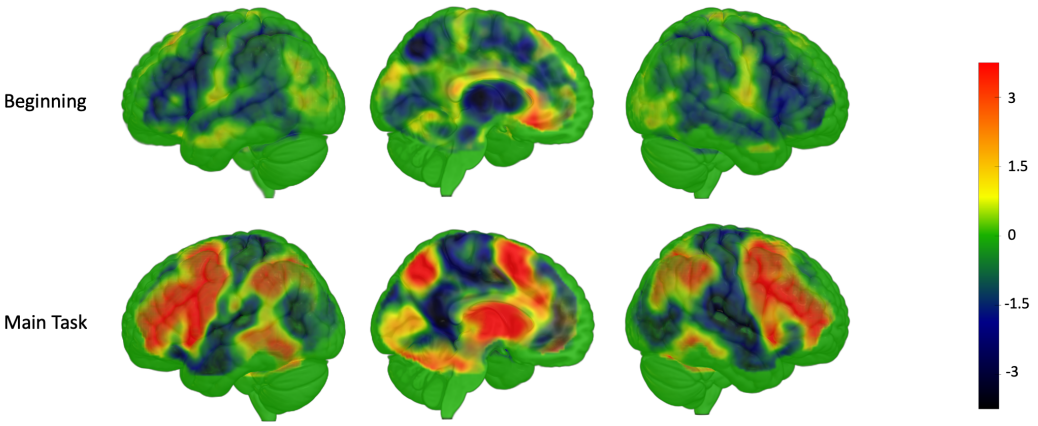

Figure 4.9: Working Memory N-Back Experiment, presented t-maps, comparing difficult > easy at the onset of task episode (beginning) and during the task episode (main task). The results indicated that MD regions exhibited increased activation during difficult conditions on main task (t thresholds corresponding to an FDR correction at $p < 0.05$ is at 2.4), without showing heightened activity at the beginning (t thresholds corresponding at $p < 0.01$ is at 3.5). Instead, MD regions on outsets (beginning) of difficult conditions, along with other brain regions, demonstrated reduced activity compared to the outset (beginning) of easy conditions when faced with challenging task demands.

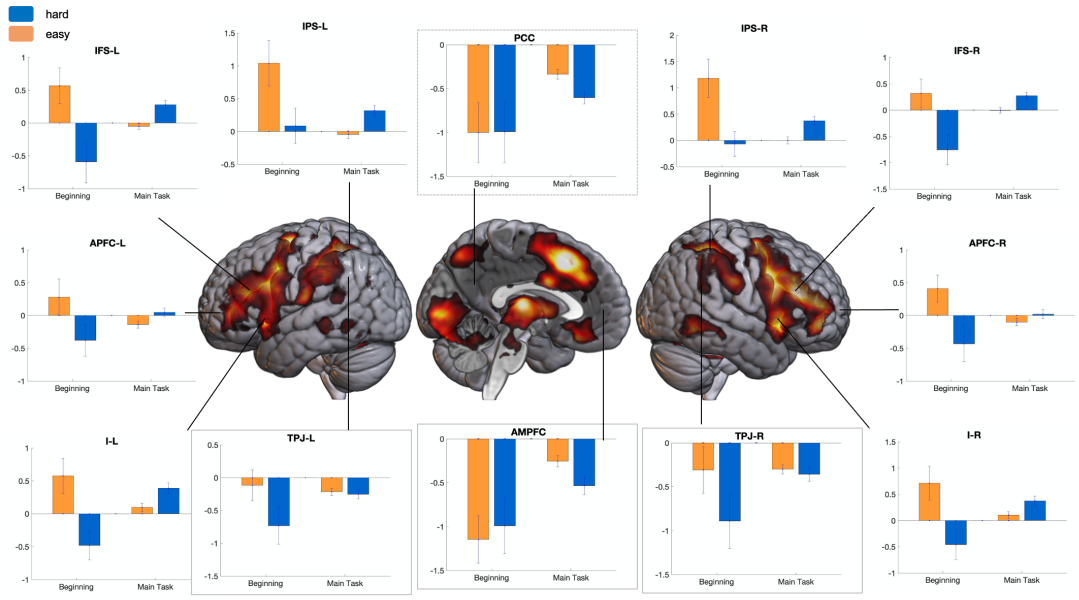

Figure 4.10: Combining the findings from the tactile decision making experiment and the working memory n-back experiment, our whole brain ANOVA analysis revealed similar patterns of activity to both experiments. Brain render highlighted regions where the impact of difficulty varied between the onset (beginning) and execution phases (main task) (FDR, $p < 0.05$). ROI plots displayed the estimated activity levels at both the beginning and throughout the main task episode for both easy and difficult conditions, with error bars indicating 95% confidence intervals. Across regions, we observed a consistent trend: at the beginning of difficult conditions, activity was lower compared to the beginning of easy conditions. However, during the main task, this pattern reversed in MD regions, with difficult conditions showing higher activity levels compared to easy conditions.

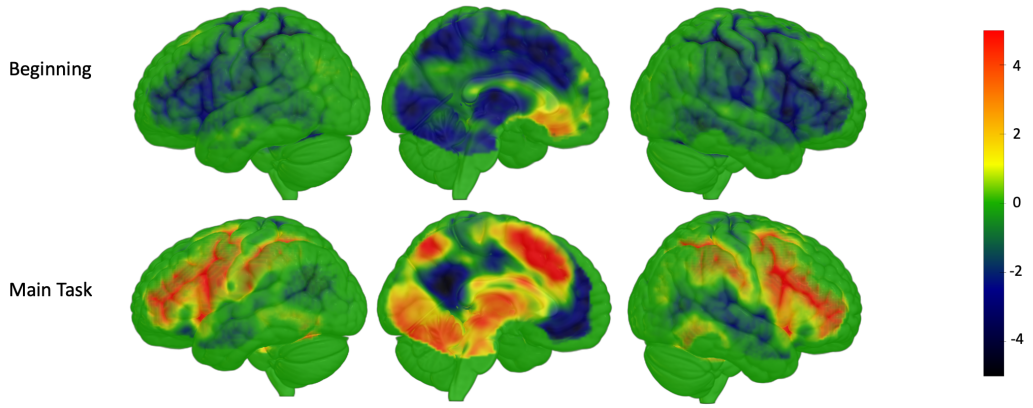

Figure 4.11: Combining the outcomes from both the tactile decision making experiment and the working memory n-back experiment, T-maps showed difficult $>$ easy contrast at the onset (beginning) and during (main task) task episodes. Interestingly, MD regions exhibited heightened activation during the difficult conditions on main task (t thresholds corresponding to an FDR correction at $p < 0.05$ is at 2.3), without any corresponding increase at their beginnings (t thresholds corresponding at $p < 0.01$ is at 3.7). In contrast, at the initiation (beginning) of difficult conditions, MD regions, alongside other brain areas, demonstrated decreased activity compared to the outset (beginning) of easy conditions.

TACTILE							
		difficulty		**step**		**difficulty x step**	
ROI name	**df**	***F***	***p***	***F***	***p***	***F***	***p***
TPJ right	1, 20	1.39	0.25	5.52	0.03	0.5	0.49
TPJ left	1, 20	3.83	0.06	0.94	0.34	1.98	0.18
AMPFC	1, 20	1.2	0.29	14.7	0.001	0.34	0.56
PCC	1, 20	0.53	0.47	7.79	0.01	0.22	0.64
APFC right	1, 20	10.4	0.004	0.09	0.76	11.8	0.003
APFC left	1, 20	6.27	0.02	0.008	0.93	8.88	0.007
IFS right	1, 20	3.57	0.07	0.0006	0.98	8.87	0.007
IFS left	1, 20	3.71	0.07	2.22	0.15	7.79	0.01
IPS right	1, 20	5.13	0.03	14.2	0.001	8.44	0.009
IPS left	1, 20	3.4	0.08	10.6	0.003	5.42	0.03
AI right	1, 20	5.96	0.02	1.36	0.26	12.9	0.002
AI left	1, 20	3.6	0.07	0.38	0.54	9.57	0.005

Table 4.1: Tactile decision making experiment, fMRI results for repeated measures of ANOVA. Region of Interest (ROI) names are bilateral inferior frontal sulcus (IFS), bilateral intraparietal sulcus (IPS), bilateral anterior insula extending in the frontal operculum (AI), bilateral anterior pre-frontal cortex (APFC), posterior cingulate cortex (PCC) and anteromedial pre-frontal cortex (AMPFC), bilateral temporoparietal junction (TPJ).

4.4 Discussion

Our study has successfully illustrated how different levels of difficulty conditions incorporated into extended tasks elicit distinct patterns of neural activity at the beginning of task episodes and throughout the task episode course, as evidenced by the findings from the line orientation fMRI experiment. Hence, our results also align with those obtained from the line orientation pupil dilation experiment, which provide complementary insights into the psychophysiological representations of cognitive demand [263, 269].

In order to ensure the robustness and generalizability of our previous findings across diverse task settings, we expanded our investigation through the implementation of two additional experiments. These experiments were meticulously designed with unique task paradigms, differing from those employed in the initial

N-BACK							
		difficulty		**step**		**difficulty x step**	
ROI name	**df**	***F***	***p***	***F***	***p***	***F***	***p***
TPJ right	1, 20	4.76	0.04	0.01	0.92	3.34	0.08
TPJ left	1, 20	4.20	0.05	1.40	0.25	4.90	0.04
AMPFC	1, 20	0.01	0.90	0.34	0.57	2.63	0.12
PCC	1, 20	0.66	0.42	0.76	0.39	0.25	0.62
APFC right	1, 20	0.62	0.44	0.10	0.75	4.14	0.05
APFC left	1, 20	0.20	0.66	0.40	0.53	4.90	0.04
IFS right	1, 20	6.54	0.02	13.5	0.001	16.0	0.0006
IFS left	1, 20	6.60	0.02	10.4	0.004	23.2	0.0001
IPS right	1, 20	3.0	0.10	5.16	0.03	20	0.0002
IPS left	1, 20	2.0	0.17	0.50	0.49	26.1	5.3055e-05
AI right	1, 20	4.75	0.04	2.0	0.17	9.44	0.006
AI left	1, 20	5.11	0.03	2.61	0.12	13.8	0.001

Table 4.2: Working memory n-back experiment, fMRI results for repeated measures of ANOVA. Region of Interest (ROI) names are bilateral inferior frontal sulcus (IFS), bilateral intraparietal sulcus (IPS), bilateral anterior insula extending in the frontal operculum (AI), bilateral anterior pre-frontal cortex (APFC), posterior cingulate cortex (PCC) and anteromedial pre-frontal cortex (AMPFC), bilateral temporoparietal junction (TPJ).

studies. In each of these experiments, participants were assigned with completing sequences of tasks categorized as easy and difficult.

These conditions consisted of multiple parts, each presenting participants with specific cognitive challenges tailored to the experimental conditions. By incorporating a range of task complexities, we aimed to capture the cognitive processing across various contexts. The participants' engagement in both easy and difficult conditions allowed us to examine how cognitive performance differed under varying levels of task difficulty. By systematically manipulating the complexity of the tasks presented, we aimed to gain a comprehensive understanding of cognitive processes across a spectrum of cognitive demands.

The tactile decision making experiment and the auditory n-back working memory experiment employed distinct paradigms to assess cognitive functions. In the

TACTILE and N-BACK							
		difficulty		**step**		**difficulty x step**	
ROI name	**df**	***F***	***p***	***F***	***p***	***F***	***p***
TPJ right	1, 20	4.33	0.05	2.75	0.11	2.63	0.12
TPJ left	1, 20	7.82	0.01	1.6	0.2	6.57	0.02
AMPFC	1, 20	0.33	0.57	8.21	0.009	2.50	0.13
PCC	1, 20	0.92	0.35	4.91	0.04	0.37	0.55
APFC right	1, 20	11.4	0.003	0.008	0.93	16.5	0.0006
APFC left	1, 20	5.61	0.03	0.07	0.79	14.7	0.001
IFS right	1, 20	8.83	0.008	6.06	0.02	19.3	0.0003
IFS left	1, 20	13.4	0.002	0.71	0.41	32.2	1.482e-05
IPS right	1, 20	8.47	0.009	1.42	0.25	23.2	0.0001
IPS left	1, 20	4.73	0.04	3.1	0.09	18.3	0.0003
AI right	1, 20	9.64	0.006	0.1	0.75	18.3	0.0004
AI left	1, 20	9.3	0.006	0.67	0.42	23.1	0.0001

Table 4.3: Tactile decision making experiment and working memory n-back experiment results combined, fMRI results for repeated measures of ANOVA. Region of Interest (ROI) names are bilateral inferior frontal sulcus (IFS), bilateral intraparietal sulcus (IPS), bilateral anterior insula extending in the frontal operculum (AI), bilateral anterior pre-frontal cortex (APFC), posterior cingulate cortex (PCC) and anteromedial pre-frontal cortex (AMPFC), bilateral temporoparietal junction (TPJ).

tactile decision making experiment, participants engaged in trials that required them to make judgments based on tactile sensations, specifically regarding the size of objects. These trials were categorized into easy and difficult conditions, varying in the complexity of the tactile judgments required. Participants were tasked with determining the large shape between different sized shapes presented to them, with the difficulty level determined by factors such as the magnitude of size differences between shapes.

The auditory n-back working memory experiment involved participants engaged at evaluating n-back tasks. Participants were presented with auditory stimuli consisting of sequences of items and were required to recall whether the current stimulus matched the one presented n steps back in the sequence. In this experiment, participants undertook both easy and difficult task conditions. Easy

conditions involved a lower working memory load, such as the 1-back task, while difficult conditions required participants to perform more difficult tasks, such as the 3-back task.

Thus, while both experiments assessed cognitive processes, they differed in the sensory modalities utilized (tactile sensations vs. auditory stimuli) and the specific cognitive functions targeted (tactile decision making vs. auditory working memory). Both experiments included difficult and easy conditions.

Our study focused on investigating how the brain responds to cognitive tasks of varying difficulty levels, particularly within regions associated with cognitive control, such as the MD regions and DMN [338, 339, 340, 341, 275, 342]. Through our observations and analyses, we identified consistent patterns in neural activity across these regions. Specifically, when participants engaged in difficult tasks, we noted that the initial fMRI response of these tasks was consistently lower compared to easy tasks. This finding suggests that the brain's initial reaction to challenging cognitive tasks involves a reduction in fmRI activation within the MD regions and DMN. While the initial response to challenging tasks was characterized by lower neural activation, we observed a contrasting trend in sustained activity as the conditions progressed. Specifically, during the subsequent execution of these conditions, MD regions exhibited higher levels of fMRI activity in difficult conditions compared to easy ones. This finding suggests that as participants continued to engage with challenging tasks over time, there was an increase in the activation of MD regions.

The distinction in the effects of difficulty at different stages of execution specifically, comparing activity at the beginning versus during subsequent execution was found to be significant across nearly all MD regions. This highlights the dynamic nature of neural responses to varying levels of cognitive demand throughout the course of task execution [69]. This shift in sustained activity highlights an intriguing aspect of the brain's response to cognitive demands. While the initial response may involve a reduction in neural activation, likely reflecting an adaptive mechanism to allocate resources efficiently, the sustained processing of challenging tasks

necessitates heightened activation in MD regions. The observed increase in neural activity during the execution of difficult conditions underscores the dynamic nature of cognitive processing and the brain's capacity to adapt to changing task demands [343, 269]. It suggests that as participants delve deeper into challenging cognitive tasks, MD regions become more engaged, potentially reflecting the allocation of additional cognitive resources to meet the demands of the task [18].

This observation is particularly intriguing as it sheds light on the brain's adaptive response to cognitive demands. When faced with a task that requires more cognitive resources and processing, such as distinguishing between complex stimuli or engaging in demanding cognitive tasks, the brain may initially exhibit a subdued neural response [69, 18]. This initial reduction in neural activation may reflect an adaptive mechanism aimed at conserving resources and optimizing cognitive efficiency. The consistent nature of this pattern across MD regions and DMN underscores its robustness and reliability. Regardless of the specific cognitive task or context, we observed a similar trend of reduced neural activation at the onset of difficult conditions across these brain regions. This suggests that the observed phenomenon is not specific to any particular task but rather represents a fundamental aspect of how the brain responds to cognitive challenges.

Overall, our findings provide valuable insights into the neural dynamics underlying cognitive processing and highlight the brain's adaptive mechanisms in the face of varying task difficulties. Moreover, this contrasting trend in sustained activity provides valuable insights into the temporal dynamics of neural processing during cognitive tasks. Further research in this area could delve deeper into the mechanisms driving these observed patterns and their implications for cognitive performance and functioning.

Chapter 5

General Discussion

When we find ourselves juggling numerous tasks simultaneously, attending events while managing multiple tasks and trying to remember a plethora of information, our performance tends to suffer [344]. This decline in performance suggests that our cognitive resources, which are crucial for various mental activities, become spread thin across these tasks [140, 345]. These resources are essential for all sorts of cognitive processes and are limited in nature. The more demanding or more difficult a task is on these cognitive resources, the higher its cognitive load [346, 347, 348].

Extended tasks that includes many minor tasks, involve the concurrent execution of multiple complex actions [140]. These tasks place a significant burden on cognitive resources due to the intricate management of various actions and their associated demands [349]. When individuals engage in such tasks, their cognitive processes perceive them as cohesive units rather than separate actions. This cognitive integration is facilitated by specialized cognitive programs that organize, integrate, and regulate the multiple constituent actions seamlessly [350].

Understanding the intricacies of cognitive load in extended tasks can inform the development of strategies to optimize performance and mitigate cognitive overload. By recognizing how cognitive resources are allocated throughout the

duration of a task, individuals can better manage their workload and enhance their efficiency. In essence, cognitive load in extended tasks stems from the complex orchestration of multiple actions as an integrated unit [351, 139, 231]. The activation of cognitive mechanisms at the task's inception sets the stage for efficient execution, with cognitive mechanisms' load diminishing as different segments of the task are completed. This dynamic allocation of cognitive resources is crucial for effective task management and performance optimization.

The exploration of cognitive load and its neural underpinnings reveals a rich tapestry of interactions between psychophysiological markers, neural responses, and cognitive processes [352]. We aimed to challenge the prevalent assumption that cognitive load operates as a unitary construct. Our study contributes to this understanding by unraveling the intricate dynamics of cognitive load and shedding light on the relationship between psychophysiological markers, such as pupil dilation, and neural activity in the multiple demand (MD) regions and the default mode network (DMN). We sought to unravel the intricate patterns underlying cognitive load.

The findings of our study challenge the conventional notion of cognitive load as a unitary construct, highlighting the importance of considering task specific factors in understanding cognitive demands [353, 354]. Contrary to expectations, we observed coherent patterns of pupil dilation and fMRI activation under high cognitive load (difficult) and low cognitive load (easy) conditions during different phases of the tasks on line orientation experiments. Also, fMRI activation patterns showed categorically different activations during trial beginnings and during trial course on tactile decision making and auditory n-back experiments.

All fMRI experiments indicated that for difficult conditions, while the initial phase appears to down-regulate MD and TPJ activity under difficult conditions, the execution phase requires a robust up-regulation to sustain the increased cognitive load. The significant interaction between task phase and difficulty confirms that the effect of difficulty on neural activation is not uniform but dynamically modulated across the extended task. The opposing activation patterns at beginning and during task episodes underscore that the brain employs different

strategies at distinct stages of task performance. These adaptive mechanisms likely optimize cognitive resource allocation by reducing unnecessary neural engagement at task onset and then mobilizing greater control processes during task execution. Moreoever, pyschophysiological markers, in this case pupil dilation, showed similar dilation patterns with the fMRI activation patterns.

On the line orientation experiments, participants engaged in various cognitive tasks while their pupil dilation and brain activity were monitored. Task A and Task B were designed to manipulate working memory load, with Task A representing one set of cognitive demands and Task B representing another. By analyzing pupil dilation and fMRI responses during these tasks, we aimed to discern any distinct patterns associated with differing levels of cognitive load.

While pupil dilation decreased on high cognitive load (difficult) during Task B presentation (step 1), it increased on high cognitive load (difficult) during Task A presentation (step 2). On the contrary, pupil dilation increased on low working memory load (easy) condition during Task B presentation (step 1) and decreased on low working memory load (easy condition) during Task A presentation (step 2). These findings suggest that psychophysiological markers manifests heterogeneously across distinct cognitive load that have different levels of difficulty, reflecting the multifaceted nature of cognitive processing.

Our fMRI results for the line orientation experiment showed the same pattern of activation on many MD and some DMN regions (bilateral TPJ) as pupil dilation results. In the multiple demand regions, where decreased activation patterns occurred on high cognitive load (difficult) condition during Task B presentation (step 1), while increased activation patterns occurred on low cognitive load (easy) condition. Remarkably, this pattern reversed during Task A presentation (step 2). This dynamic shift in activation patterns underlines the complexity of cognitive load and its complex response to different cognitive loads. On the other hand, while default mode regions generally exhibited a deactivation patterns under high cognitive load (difficult) and low cognitive load (easy) conditions, diverse deactivation patterns were observed at the beginning and during trials. These variations underscore the complex nature of cognitive load and highlight the need

to consider different cognitive demands when assessing neural responses. In terms of DMN, TPJ showed similar deactivation patterns as MD regions. Bilateral TPJ on low cognitive load condition (easy) showed less deactivation or more activation on task B presentation (step 1) compare to task A presentation (step 2) and on high load condition (difficult) showed more deactivation on task B presentation (step 1) compare to task A presentation (step 2).

The fMRI results on the tactile decision making experiment and auditory n-back experiment reflected same activation and deactivation patterns between easy and difficult conditions during trial beginnings and during trial course. As explained, these two experiments included separate tasks compared to line orientation experiments. However during trial beginnings, difficult condition resulted with an decreased activation pattern in MD regions and some DMN regions. Nevertheless, during trial course, it showed increased activation patterns overall MD regions and some DMN regions. As it was the case in line orientation experiments, activation and deactivation patterns reversed when the task condition changed from difficult to easy between initiation of task episodes and during task episodes. During trial beginnings, easy condition resulted with an increased activation pattern in MD regions and some DMN regions. In terms of DMN in the line orientation fMRI experiment, bilateral TPJ showed similar deactivation patterns as MD regions. Bilateral TPJ on easy condition showed less deactivation during trial beginnings compare to during trial course and on difficult condition showed more deactivation during trial beginnings compare to during trial course. Our results are consistent through all fMRI experiments. Since the activation patterns of the MD regions and bilateral TPJ showed the same trend of activation in all three fMRI experiments, our investigation into the neural correlates of cognitive load revealed dynamic interactions between the MD regions and the DMN, suggesting that different regions of the brain outside the MD or DMN network can show activation as they are part of one of these networks on various tasks [251]. Therefore, this suggestion challenges the traditional dichotomous views of brain function. While previous research has emphasized the antagonistic relationship between these networks [355, 356, 357, 290, 358], our findings suggest the presence of a more integrated model of cognitive processing. We observed

heightened activation within MD regions and DMN under conditions of increased cognitive load during task episodes consistent with MD regions' role in cognitive control and attentional processing [359, 360]. However, we also observed concurrent deactivation within the MD regions and DMN [314], indicating a dynamic interplay between internally directed processes and externally oriented cognitive demands. These findings suggest that MD regions and the DMN are not isolated entities [311] but engage in dynamic interactions, reflecting the brain's capacity for flexible cognitive processing [312].

Moreover, our pupil dilation and fMRI results, clearly demonstrate that psychophysiological markers and neural activations both show distinct activation patterns during trial beginnings and during trial course for various cognitive loads, which are easy versus difficult conditions, within similar tasks and these activation patterns reoccurring throughout distinct experiments. Hence, pupil dilation could be considered as a valid representation of cognitive load as neural representations [361, 362, 363, 364, 365, 366].

This thesis provides a multidimensional exploration of cognitive load, integrating psychophysiological markers and neural activity across diverse task paradigms. Activation trends in multiple demand regions and default mode network provided compelling evidence challenging the notion of cognitive load as a unitary construct [365, 362, 358, 79, 367, 368]. The findings highlight the brain's complexity, as evidenced by the dynamic interactions between MD regions and the DMN in response to varying task demands. The observation of consistent activation patterns across multiple experiments underscores the robustness of these neural mechanisms, while the complementary insights from pupil dilation measurements validate the utility of psychophysiological markers in cognitive research [312, 361, 369]. By uncovering distinct patterns in pupil dilation and fMRI responses across different cognitive tasks, we shed light on the diverse ways in which cognitive demands affect neural and psychophysiological processes [363, 364, 366, 370, 371, 372]. The brain's ability to allocate resources dynamically, balancing efficiency with performance, speaks to its intricate design and resilience. By uncovering these patterns, this thesis not only advances theoretical understanding but also paves the way for further research aimed at unraveling

the intricacies of cognitive load and its implications for cognitive functioning [358, 369]. Further understanding these complex activation trends is crucial for developing more precise models of cognitive load and its impact on cognitive functioning.

Thus, the findings of this thesis have significant implications for our understanding of cognitive load, neural resource allocation, and the dynamic interaction between multiple demand (MD) regions and the default mode network (DMN). By demonstrating that cognitive load is not a unitary construct but instead consists of distinct neural mechanisms that vary across task phases, this research challenges traditional models that separate externally and internally directed processes. The discovery that certain DMN regions, such as the temporoparietal junction (TPJ), exhibit activation patterns akin to MD regions under specific cognitive demands suggests a more integrated neural framework for executive control. Furthermore, the strong correlation between pupil dilation and fMRI activations highlights the potential for psychophysiological markers as reliable proxies for cognitive effort, paving the way for more accessible, non-invasive cognitive monitoring. These insights have practical applications in cognitive training, workload management, and clinical interventions, particularly in populations with attentional deficits or executive dysfunctions. By refining models of cognitive flexibility and resource allocation, this research informs the development of adaptive strategies for enhancing mental efficiency in high-demand environments, from educational settings to professional workspaces. Ultimately, these findings contribute to a more complex perspective on how the brain balances attentional focus, executive demands, and internal thought processes, offering new directions for both theoretical and applied neuroscience.

In terms of limitations, the tasks employed in this study, such as line orientation, tactile decision-making, and auditory n-back tasks, were carefully chosen to isolate specific aspects of cognitive load. However, these controlled paradigms may not fully capture the complexity of real-world cognitive demands. Future research could incorporate more ecologically valid tasks, if possible in real life environments that would enable multitasking scenarios or decision-making in naturalistic environments, to test the applicability of findings in everyday contexts.

Future studies could also investigate cognitive load across a broader range of sensory modalities and task contexts. For instance, exploring the neural and psychophysiological responses to emotionally charged tasks, social interactions, or complex problem-solving scenarios would provide a richer understanding of how cognitive load operates in diverse settings. Tasks involving multitasking or decision-making under uncertainty could also illuminate how the brain allocates resources in more complex environments. Video game like features while designing experiments or simply using online video games could be successful to imitate these real life settings.

In addition, the participants were predominantly young, educated, and healthy individuals. Although this homogeneity reduced variability and increased statistical power, it limits the generalizability of findings to broader populations, including older adults, children, or clinical groups [312]. Investigating how age, education, and neurological or psychological conditions influence cognitive load responses would provide a more comprehensive understanding of these processes. Although we integrated psychophysiological measurements, such as pupil dilation, with fMRI to enhance temporal resolution, the inherent limitations of fMRI in capturing rapid neural dynamics remained. Future studies could address this by incorporating complementary methods, such as EEG and MEG, to achieve both high spatial and temporal resolution. Furthermore, Longitudinal research could examine how cognitive load responses evolve over time, particularly in aging populations or individuals undergoing cognitive training [361, 362]. Comparative studies involving clinical populations, such as individuals with ADHD, schizophrenia, or traumatic brain injury, could reveal how cognitive control and neural dynamics differ across conditions and inform targeted interventions [363, 364, 366].

Looking ahead, addressing the limitations of this research and embracing the outlined future directions will be crucial for building on these insights. Investigating cognitive load across broader populations, diverse task modalities, and real-world contexts will deepen our understanding of how the brain navigates the complexities of modern life. Moreover, integrating advanced methodologies and exploring individual differences hold promise for tailoring interventions and optimizing cognitive performance in a wide array of settings. In conclusion, this

thesis underscores the importance of a multidisciplinary approach to studying cognitive load. By bridging neural, psychophysiological, and behavioral perspectives, it lays a foundation for future research aimed at unraveling the complexities of human cognition and fostering innovations to enhance mental performance and well-being.

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