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Review

Neural correlates of visuospatial consciousness in 3D default space: Insights from contralateral neglect syndrome



Ravinder Jerath*, Molly W. Crawford

Augusta Women's Center, Augusta, GA, USA

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ABSTRACT

One of the most compelling questions still unanswered in neuroscience is how consciousness arises. In this article, we examine visual processing, the parietal lobe, and contralateral neglect syndrome as a window into consciousness and how the brain functions as the mind and we introduce a mechanism for the processing of visual information and its role in consciousness. We propose that consciousness arises from integration of information from throughout the body and brain by the thalamus and that the thalamus reimages visual and other sensory information from throughout the cortex in a default three-dimensional space in the mind. We further suggest that the thalamus generates a dynamic default three-dimensional space by integrating processed information from corticothalamic feedback loops, creating an infrastructure that may form the basis of our consciousness. Further experimental evidence is needed to examine and support this hypothesis, the role of the thalamus, and to further elucidate the mechanism of consciousness.

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1. Introduction

The nature of consciousness and how the brain functions as the mind are questions that continue to evade explanation by neuroscience. These questions have been pondered for millennia by scientists, philosophers, and layman alike but we have

* Corresponding author. Address: Augusta Women's Center 2100 Central Ave, Suite #7, Augusta, GA 30904, USA.
 E-mail address: Rj605r@aol.com (R. Jerath).

just begun to discover the neural correlates and possible mechanisms of consciousness. Furthering our understanding of how consciousness arises and how the brain acts as the mind will greatly impact our understanding of the inner workings of the brain and will advance the field of neuroscience as a whole. In the past, many scientists avoided studying this topic because so much of consciousness is subjective, they did not think it could be studied using objective experimental methods (Hendriks-Jansen, 1996). Recent research has established that many areas of the brain are involved in consciousness but we will be focusing on the visual and spatial processing aspects of consciousness. To examine this topic we must first start by defining consciousness within a scientific framework, rather than from a philosophical or religious view. From a neurological standpoint, consciousness is a waking state that lies on a spectrum from waking to sleep to coma (De Sousa, 2013). However we will focus more on another usage in which consciousness refers to subjective experience and feelings, body ownership, sense of self, and body schema. Body ownership is the perception of one's own body (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007) and body schema is a representation of the position of the body and its parts within a space, including the length of limbs, their arrangement in space, and the shape of the body surface (Holmes & Spence, 2004; Macaluso & Maravita, 2010; Maravita, Spence, & Driver, 2003). The term body schema was coined by Sir Henry Head in order to discuss damaged spatial representations of the body after parietal lobe damage (Head, 1911). We too will be examining parietal lobe damage in contralateral neglect syndrome and we will use this syndrome and visuospatial processing as windows into the process of consciousness. Crick and Koch proposed that an essential function of consciousness is visual awareness, making the best interpretation of the visual scene in a compressed form, and relaying this to other areas of the brain (Crick & Koch, 1995) so visual processing is a vital aspect of consciousness to examine.

2. Visual and spatial processing in the parietal lobe and related areas

The parietal lobe is important for spatial processing, spatial orientation, and spatial attention or salience (Colby & Goldberg, 1999; Goldberg, Bisley, Powell, & Gottlieb, 2006; Kusunoki & Goldberg, 2003). Studies on macaque monkeys have shown that groups of neurons in the parietal cortex represent different areas of space. The lateral intraparietal area consists of a map of neurons representing the retinally-mapped coordinates of spatial locations and spatial attention (Goldberg et al., 2006; Kusunoki & Goldberg, 2003). The ventral intraparietal area receives sensory information from visual, somatosensory, auditory, and vestibular sensory systems (Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005). Medial intraparietal neurons encode location while in this experiment premotor neurons encoded the relative positions of the hand, eye, and the goal (Pesaran, Nelson, & Andersen, 2006). A study on the ventral premotor cortex of monkeys found that when an object was shown within the visual receptive field of individual neurons and the lights were turned off and the object was removed, a group of neurons still responded in the dark as if the object was still visible (Graziano, Hu, & Gross, 1997). These neurons exhibited object permanence, so that even though the object was no longer visible, the brain still “thought” it was there (Graziano et al., 1997). The lateral intraparietal area and medial intraparietal areas in monkeys can be equated to the ‘parietal eye field’ and ‘parietal reach region’ in humans respectively. Neurons in these areas represent visual space and remap this visual space when the eyes move, in a gaze-centered frame (Medendorp, Goltz, Vilis, & Crawford, 2003). Another study on monkeys found that when shown arrangements of squares and then shown that arrangement with a missing square, the activity of many 7a neurons in the monkey parietal lobe varied systematically with the position of the missing square (Chafee, Crowe, Averbeck, & Georgopoulos, 2005). This neuronal activity did not correlate with the retinal location of the square or the direction of motor responses, further supporting that parietal neurons are involved in neural representations of space and that they code this spatial information onto visual stimuli information (Chafee et al., 2005).

The lateral intraparietal area is interconnected with the frontal eye field (FEF) and other areas of the visual cortex and projects to intermediate layers of the superior colliculus (Andersen, Asanuma, Essick, & Siegel, 1990; Lynch, Graybiel, & Lobbeck, 1985). The receptive field for sharp foveal vision is only 2–5 degrees so the eyes or head must scan an entire scene in saccades (Trehub, 2007). The parietal cortex, specifically the lateral intraparietal area, is highly involved in the neural processing of saccadic eye movements, likely due to its function in creating a salience map (Bisley & Goldberg, 2003). In addition, distinct electrophysiological patterns were observed for leftward but not rightward saccades, consistent with known right hemispheric dominance in spatial attention (Ptak, Camen, Morand, & Schneider, 2011). In addition, Raffi and Siegel found that the internally generated area of attention in monkeys is correlated with an 800–860 μm patchy topographical map on the surface of the inferior parietal lobe (Raffi & Siegel, 2005). This was evident because there was modulation of this area in the presence of a cue location but not from the presence of a cue alone.

Studies on tool use have shown that body schema can be modified (Berti & Frassinetti, 2000; Iriki, Tanaka, & Iwamura, 1996; Angelo Maravita & Iriki, 2004). In the caudal postcentral gyrus within the parietal lobe, there are neurons that appear to code for the schema of the hand and the visual receptive fields of these neurons change to include the tool being used (Iriki et al., 1996). Another study, on blind cane users, found that the cane extended peri-hand space of the users (Serino, Bassolino, Farnè, & Ládavas, 2007). In addition, extrapersonal or far space can remap as peripersonal or near space when using tools (Berti & Frassinetti, 2000).

3. Contralateral neglect syndrome

The effects of contralateral neglect (CN) syndrome provide a window into the inner workings of visuospatial orientation, default 3D space, and consciousness. CN syndrome is a neurophysiologic condition in which there is damage to one side of

the brain and the resultant hemispatial neglect is contralateral to the damaged hemisphere. The most common damage leading to hemispatial neglect is a lesion in the right parietal lobe leading to visual neglect of the left side of the visual field (Kerkhoff, 2001). These patients will bump into objects or obstacles on their left side (Unsworth, 2007), if asked to draw an object they will draw only the right side (Kerkhoff, 2001), they may read only the right pages of books (Halligan & Marshall, 1998), or they may neglect the left side of their body (Kerkhoff, 2001). Some researchers propose that the right superior temporal gyrus is associated with hemineglect but this has been challenged (Mort et al., 2003) and remains controversial. It has been proposed that hemispatial neglect occurs more commonly after damage to the right hemisphere because the right hemisphere is more involved in spatial perception and spatial memory whereas the left hemisphere is more specialized for functions like language; it appears that there is processing of the right visual field in both hemispheres. If there is a loss of function in the left hemisphere, the right hemisphere is able to compensate for that, but if there is damage to the right hemisphere the left hemisphere is not able to compensate (Iachini, Ruggiero, Conson, & Trojano, 2009).

In an experiment comparing thermal pain stimuli in CN patients versus normal controls, a significantly larger proportion of contralateral neglect patients did not experience any thermal pain stimuli on their left side while others mislocated the pain as coming from the unaffected right side. Often this pain was also misidentified as to whether it was hot or cold. This study demonstrates the strong effects contralateral neglect has on spatial attention and perception (Liu et al., 2011) and although they do not have peripheral nerve damage many cannot detect sensory information on their left side or they mislocate it to their unaffected side. Some patients even fail to use their contralateral limbs but have intact motor and nerve function (Kerkhoff, 2001).

Studies have shown that information from the neglected side in CN patients is unconsciously processed to some degree. Semantic priming studies have found that stimuli that was unreported from the left side of the visual field significantly speeded responses to a subsequent word if it was related to the neglected stimuli, such as tree and apple or bat and ball, when compared to unrelated items like bed and apple (McGlinchey-Berroth, Milberg, Verfaellie, Alexander, & Kilduff, 1993; McGlinchey-Berroth et al., 1996). These studies suggest that neglected visual information is not filtered out early on, as some researchers have suggested, instead there may be only a partial disruption of the pathways responsible for visuospatial processing. The researchers suggest that one possibility for this semantic priming phenomenon is that in hemispatial neglect visual stimuli in the extinguished field is perceived but cannot reach conscious awareness (McGlinchey-Berroth et al., 1993). We propose that this visual information is lost when it is processed by or attempted to be processed by the damaged parietal lobe. The parietal lobe is not able to spatially map the visual information so when this information is sent back to the thalamus via feedback loops it is not projected within the 3D default space and therefore does not rise to conscious awareness.

CN also affects visual memory. In one experiment, patients with CN from Milan were asked to describe the Piazza del Duomo, a well-known square. First they were asked to imagine the square from the viewpoint looking out from the cathedral located in the center of the square, and then from the viewpoint looking at the cathedral. During the first description the patients neglected to describe places and streets on the left side of the square and when asked to shift their perspective 180 degrees to the second imagined view they omitted places and streets on the left side of the new imagined vantage point that they had just described during the previous view (Bisiach & Luzzatti, 1978). More recent studies, have confirmed these deficits in spatial working memory and visual memory in patients with contralateral neglect (Luukkainen-Markkula, Tarkka, Pitkänen, Sivenius, & Hämäläinen, 2011).

4. Previously proposed mechanisms of neglect in contralateral neglect syndrome

There are multiple hypotheses regarding the mechanism underlying CN. Confounding the issue is that many CN patients have varying combinations of deficits including varying levels of motor impairment, sensory dysfunction, and personal and/or peripersonal neglect (Buxbaum et al., 2004) making it difficult to pinpoint the exact mechanism. Differing theories hypothesize that CN may involve interrupted sensory, and/or attention processes, as well as other disrupted processes (Smania et al., 1998). Hypotheses proposing disrupted attention processing suggest that patients are unable to direct attention away from the right side to the left, resulting in neglect of the left side (Bartolomeo & Chokron, 2002; Losier & Klein, 2001; Posner, Walker, Friedrich, & Rafal, 1984). Other researchers suggest that there is a disruption in the balance of directing attention between the left and right hemispheres (Kinsbourne, 1993) resulting in hyper-attention to the right side. They propose that the mechanisms that orient attention to the right visual sphere and right side of the body may go unchecked when the damaged right side no longer orients attention to the left (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005), causing patients to orient and turn more to the right when exploring their visual surroundings (Kinsbourne, 1993). However, this hypothesis was supported by animal studies in which lesions were experimentally induced in monkeys (Kinsbourne, 1993) but this has since been found to be unsupported in humans (Karnath, Niemeier, & Dichgans, 1998). A study on exploration of visual space of CN patients found that they exhibited the same coordinated eye and head movements as healthy controls (Karnath et al., 1998). The CN patients did not turn more and more to the right, rather their center of orienting, gaze, position of eyes in their head, and head were shifted slightly to the right space when compared to healthy controls (Karnath et al., 1998). These researchers proposed that patients with CN may have an altered neural representation of space, specifically in the horizontal dimension rather than hyper-attention to the right side (Karnath et al., 1998). The parietal and occipital cortexes have been shown to both contribute to the perception of straight ahead orientation and perceived

body midline (Ferber & Karnath, 1999). In this study patients with neglect had a shifted perception of straight ahead towards the ipsilateral side while patients with hemianopia, decreased vision due to stroke or other brain damage, had a shifted perception of straight ahead orientation to the contralateral side. Lesions in the same hemisphere resulting in both neglect and hemianopia had counteracting effects on perception of the body midline (Ferber & Karnath, 1999). Other researchers propose that information and stimuli compete for attention within the two hemispheres. So in CN patients stimuli on the right side wins over the left side, resulting in neglect of the left. This is supported by studies showing that increased stimuli or distracters on the right side lessens attention to the neglected left side, when compared to less stimuli on the non-neglected side (Kaplan et al., 1991).

5. Hypothesis

We propose a hypothesis that integrates many theories of consciousness into a simple model that describes how the brain acts as the mind. Insights into this mechanism have been derived from the symptoms of patients with CN that do not consciously see objects in space on their left side and whom ignore the left side of their body. Our proposed mechanism supports many aspects of the Global Workspace Theory (GWT), which can be explained using a theatre metaphor, in which consciousness is a bright light on a stage while the rest of the dark theatre represents the unconscious. This bright spot of consciousness is created from the input and feedback of unconscious sensory, executive, and other processing throughout the brain (Baars, 2005). Many models of consciousness describe specific neural correlates of consciousness but they fail to describe how a specific unifying mechanism coordinates and integrates this information. Similar to other hypotheses, we propose that the thalamus integrates and coordinates information from many different areas of the cortex. Because our hypothesis incorporates previously proposed mechanisms of consciousness, we should specify how our hypothesis differs. First we have designated the thalamus as a dynamic neural center that processes and integrates information from throughout the cortex and body to create a reimagining of 3D space. According to the GWT, consciousness arises from many anatomical hubs throughout the brain (Baars, Franklin, & Ramsøy, 2013). Our model also proposes that many areas of the brain are involved in consciousness but we designate the thalamus as a central hub in which this unconscious processed information is integrated and becomes conscious. This integrated information from throughout the brain and body is then reimagined by the thalamus in a 3D default space in our minds, resulting in the visual images we “see,” imagine, and even our sense of self, and body schema (Fig. 1). We have termed this 3D “default” space to denote that this space is intrinsic and forms automatically. In fact, 90% of the brain’s energy is used by intrinsic or default mode activity (Raichle & Snyder, 2007). We propose that the 3D default space is likely associated with the default mode network but establishing such a relationship requires further

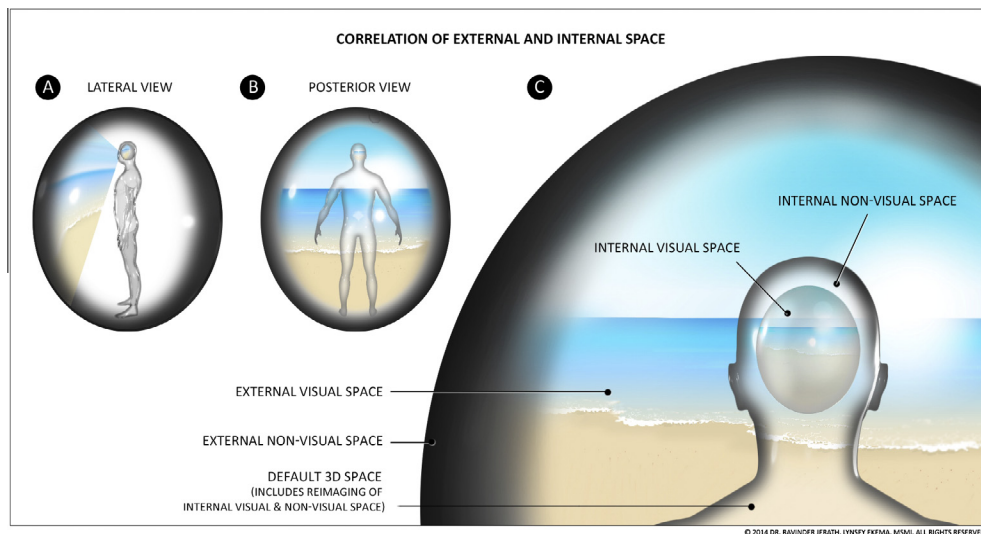


Fig. 1. Internal and external visual fields: An important aspect of consciousness is the processing of sensory information. This figure aims to show the processing of visual sensory information and the default 3D space created in the mind. The area surrounding the figure represents the external visual space and the black surrounding area represents external non-visual space. The global visual field is surrounded by this dark shading to illustrate where the figure’s visual field ends. This external visual space is seen by the eyes, processed by the brain, and an internal visual space of external visual space is reimagined within the mind, along with non-visual space. We refer to this reproduction of visual and non-visual space as the 3D default space. Note that this representation of the reimagining of space illustrates this phenomenon and is not meant to indicate any anatomical landmarks in the brain. The outline of the figure is also surrounded by dark shading to show where internal space ends and reflects how the external non-visible space is mirrored functionally within the internal non-visible space. The brain is constantly receiving internal information from throughout the body and external information via the sensory systems that contribute to the formation of consciousness, a sense of self, and a 3D default space consisting of integrated and reprojected internal and external space. The external visual and non-visual world appears separate from our internal world due to the high speed processing of corticothalamic information. This illusion allows the brain to function as the mind in a seemingly seamless reality. (Figure by Lynsey Ekema, MSML.)

investigation. Such an active electrical infrastructure likely supports visuospatial consciousness as well as body consciousness as a whole. The entire body, bounded by our skin, forms the matrix for this 3D default space. All cells of the body are electrically charged, metabolically active, and interconnected. They originate from one cell and communicate via gap junctions interconnected by intracellular and extracellular fluid (Lampe & Lau, 2004). The entire body of cells constitutes a framework that serves as a 3D default matrix on which the 3D default space and all internal and external memories are formed. The thalamus seamlessly reimages or projects processed visual and non-visual information within this space. When we refer to “reimaging” we mean the integration and subsequent representation of visual and non-visual information in the sensory apparatus within the mind. We propose that this reimaging is done by parallel processing throughout the cortex that is integrated by the reticular nucleus and other nuclei of the thalamus.

We also propose that this 3D space is reimaged in a default 3D space created by coordinated oscillations, likely from the thalamus and other areas throughout the brain. This space is not an actual “space” in the general sense but a virtual space created within the neural medium of the brain. Most models of consciousness acknowledge the role of afferent signaling but focus almost entirely on the brain and its function as the mind. Our model emphasizes the major role of afferent signaling from throughout the entire body. The human body is made up of trillions of individual cells (Bianconi et al., 2013) that communicate and act as one unit. Sensory information from throughout the body is processed and forms the body schema within this 3D default space. The thalamus, which is centrally located in the middle of the brain, integrates multisensory afferent information and duplicates the events we experience within milliseconds in our minds and allows our cognitive processing to seamlessly perform executive and motor functions in real time. Consciousness consists of internal and external experiences merging into a temporally and spatially integrated experience (Fuster, 2008) and we propose that the thalamus and corticothalamic processing are responsible for this integration. Although the entire brain and body are involved in consciousness and cognition, we propose that the thalamus is the central hub that integrates and recognizes the information processed by corticothalamic feedback loops and reimages it within the 3D default space, resulting in conscious awareness. The thalamus integrates this sensory information from throughout the body and creates a reproduction of visual and non-visual space within this 3D space, resulting in one’s body schema. When this sensory information is combined with processed information from throughout the brain it results in consciousness and a sense of self. We also propose that visual space occupies only a portion of this reimaged 3D space; the remainder is occupied by a reproduction of non-visual internal and external space. It has been proposed that normal self-awareness depends on several parallel processes including intact sensory feedback, “the ability to attend to both one’s body and the space where parts of the body may be positioned or acting,” and the ability to create a representation of the body that must be continuously modified by the processing of new information (Heilman, Barrett, & Adair, 1998). It has been proposed that anosognosia, a lack of self-awareness, that occurs in some patients with CN, is due to dysfunctions in the processing that creates this representation of the body in the mind (Heilman et al., 1998). Our model 3D default space explains these parallel processes that create a seamless and dynamic 3D space of the body and external space that is continuously modified by incoming information. Damage to the right parietal lobe in CN leads to damaged processing of sensory feedback from the left side resulting in incomplete self-awareness.

Optical illusions such as afterimages may provide evidence in support of our model of visual consciousness. Negative afterimages were thought to be due to overstimulation and desensitization of photoreceptors in the retina that cause the subject to see a negative image when the eyes are redirected at a blank space (Brindley, 1962). This was thought to be due to activation of the surrounding photoreceptors that were not being stimulated when previously viewing the original image. There is also the phenomenon of positive afterimages in which the afterimage is the same color as the original image; however, the underlying mechanism for this type of afterimage is not well understood. Experiments indicate a cortical basis for this type of afterimage rather than merely photoreceptor activity (Holcombe, MacLeod, & Mitten, 2004; Shimojo, Kamitani, & Nishida, 2001). These positive afterimages are likely representations filled-in by cortical activity (Holcombe et al., 2004) and possibly thalamic activity. Even negative afterimages have been shown to involve higher level cognitive processing. For example, studies on perceived size of negative afterimages have shown that retinal stimulation is needed to induce an afterimage but higher processing influences the perceived size (Sperandio, Lak, & Goodale, 2012). These studies are consistent with our visual consciousness model in which the external visual space is duplicated within the mind. We propose that the involvement of higher processing in the formation of afterimages suggests that afterimages may be the remnants of the original processed visual information that was reimaged within the 3D default space.

Our model is also not as brain-centric as other models of consciousness. We suggest that sensory information from throughout the body is processed so quickly that the brain and body act as one to create the experience of consciousness. Both cognitive and sensory experiences make up consciousness (Heavey & Hurlburt, 2008; Hurlburt & Heavey, 2009) and the thalamus is a central hub for integrating this information from throughout the brain and body. In addition, studies suggest that the prefrontal cortex (PFC) and frontal lobe are involved in visual processing (Peers et al., 2005) and visual perception (Libedinsky & Livingstone, 2011) and that frontal eye fields in the frontal lobe are activated early on in visual processing, suggesting that processing in the frontal lobe may occur early on and then integrate with other processed visual information (Libedinsky & Livingstone, 2011) in the thalamus (Fig. 2). The PFC has large and widespread connections to the thalamic reticular nucleus (TRN), which regulates communication between the thalamus and PFC (Zikopoulos & Barbas, 2007). In addition, the mediodorsal nucleus, the main thalamic nucleus for the prefrontal cortex, also has widespread connections to the TRN (Zikopoulos & Barbas, 2007). The TRN is likely highly involved in controlling and directing attention of the PFC and other cortical areas (Min, 2010; Zikopoulos & Barbas, 2007).

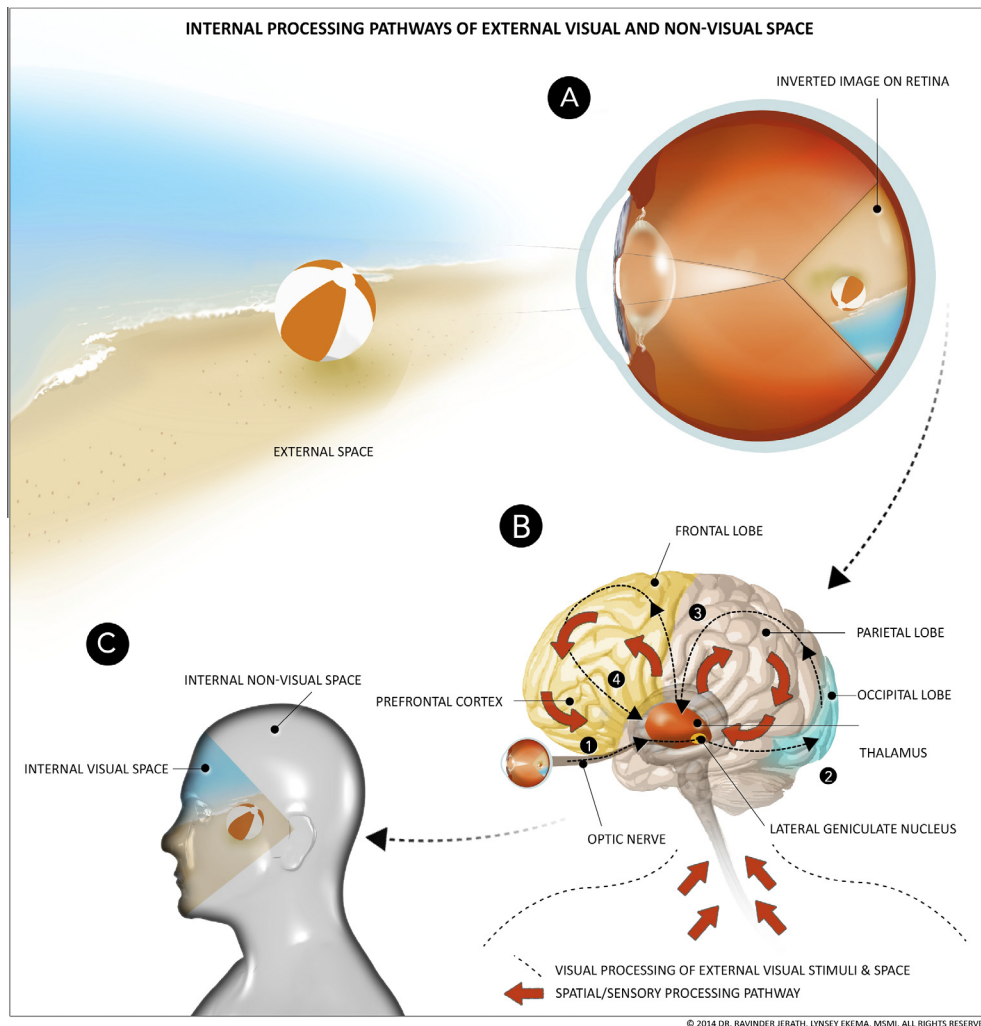


Fig. 2. Internal processing pathways of external visual and non-visual space: This figure depicts simplified processing pathways of visual and other sensory space. Light entering the eye forms an inverted image of the external visual space on the retina. This visual information passes through the optic nerve, through the lateral geniculate body and other areas of the thalamus, to the occipital lobe, the parietal lobe, and then back to the thalamus. This processed information then further processed in the frontal lobe and prefrontal cortex and back to the thalamus. This processed visual information becomes conscious when it is integrated and reimaged by the thalamus in the default 3D space. All this processing occurs in fractions of a second, so the viewer does not notice that what they are “seeing” is a processed image within their minds, rather than the actual external space. In addition to processed visual information, this default 3D space is also formed via afferent spatial/sensory input from the body. This information is involved in feedback loops between the thalamus and parietal lobe and the thalamus and frontal lobe. The thalamus integrates this processed non-visual information and forms the 3D body space within the mind. (Figure by Lynsey Ekema, MSMI.)

The thalamus used to be regarded as simply a relay station for visual information but research on corticothalamic feedback pathways have shown that the thalamus is an integral part of sensory processing (Cudeiro & Sillito, 2006; Ward, 2013) and the formation of a “cognitive map” (Cudeiro & Sillito, 2006). In fact, the thalamus may regulate cortical activity by way of phase-amplitude coupling, which may be the mechanism by which information is integrated and segregated across cortical areas (Malekmohammadi, Elias, & Pouratian, 2014). Large scale integration of information into a unified cognitive moment likely involves dynamic connections mediated by synchrony over multiple wavelengths (Cantero & Atienza, 2005; Varela, Lachaux, Rodriguez, & Martinerie, 2001). Other models have proposed that the thalamus plays a central role in consciousness. One such hypothesis proposes that the thalamic reticular nucleus modulates and coordinates thalamocortical networks, resulting in conscious awareness (Min, 2010) and many models of consciousness, such as the GWT, and visual processing models involve corticothalamic feedback mechanisms in which information is sent from the thalamus to various areas of the cortex and then back (Edelman, 2003; Saalmann & Kastner, 2011; Sillito, Cudeiro, & Jones, 2006). It has also been found that the thalamus regulates levels of consciousness and influences of the brainstem on the thalamus are essential in altering the conscious state during sleep (Steriade, 1992). The thalamus’s involvement in visual and sensory processing, its role in relaying information to areas throughout the cortex, and receiving feedback of processed information from those

cortical areas, makes the thalamus a prime candidate for the center of consciousness (Min, 2010) and sensory reimagining of external and internal space. Synchrony between the thalamus and cortex is essential for consciousness (Jones, 2009), suggesting there may be a central hub that synchronizes chaotic neural activity into conscious events (Min, 2010). GABAergic neurons are present in the visual thalamic areas of many mammal species, including humans, and the number of GABAergic neurons increases in the dorsal thalamus in species with more complex behaviors. In addition, the number of GABAergic neurons in the thalamus of various species likely indicates the increasing complexity of information processing in the thalamus (Arcelli, Frassoni, Regondi, De Biasi, & Spreafico, 1997). GABAergic neurons in the TRN have strong inhibitory connections with the dorsal thalamus and produce long-lasting feedforward inhibition in thalamic relay cells (Sun et al., 2012). The TRN regulates activity between the thalamus and the cortex via inhibition and disinhibition (Zikopoulos & Barbas, 2007). The GABAergic neurons of the TRN also play a significant role in switching between awake and sleep (Steriade, Contreras, Curro Dossi, & Nunez, 1993), suggesting their possible role in consciousness. These studies demonstrate the important role of the thalamus in processing and regulation of cortical areas, which make the thalamus a prime candidate for the center of consciousness. fMRI studies on binocular rivalry, in which dissimilar images presented to each eye compete for perceptual dominance, have shown that activity in the lateral geniculate nucleus in the thalamus reflects the subjects' percept rather than the input from both eyes (Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2005). Adjustments for visual disparities made in the brain are affected by the corticogeniculate projection which influences previously separate ocular representations in the LGN (McIlwain, 1995). This suggests that processed information from the cortex may influence the ocular representations in the LGN to create a seamless binocular representation from separate monocular images. These studies may indirectly support our hypothesis that the thalamus reimages processed visual information. In addition, studies have found that many patients with right-sided thalamic lesions experience hemineglect (Kumral, Kocaer, Ertubey, & Kumral, 1995; Ortigue et al., 2001; Schmahmann, 2003; Vallar & Perani, 1986; Watson & Heilman, 1979) and anosognosia (Kumral et al., 1995; Watson & Heilman, 1979), further supporting our hypothesis that a healthy thalamus integrates processed sensory information from corticothalamic feedback loops and perceives a dynamic 3D space. Although not indicative of causation, the contralateral neglect that is exhibited in patients with parietal or thalamus damage is consistent with our proposed visual consciousness model in which the thalamus may be the central hub that integrates processed visual and sensory information from throughout the cortex, including the parietal cortex, via corticothalamic feedback loops. These corticothalamic pathways make the thalamus a prime candidate for multisensory integration (Tyll, Budinger, & Noesselt, 2011). If the right parietal lobe is damaged the patient may experience contralateral neglect because the parietal lobe is not able to spatially map the left side of the visual field or body. If the thalamus is damaged, the thalamus is not able to integrate and reimage the processed information from the parietal lobe and other cortical areas within the 3D default space, resulting in neglect.

Contrary to conventional views, thalamocortical transmissions from the thalamus to cortical areas, including the PFC, are strong, fast, and long-lasting and are involved in the regulation of cortical activity (Cruikshank et al., 2012). Information processed, almost instantaneously, by corticothalamic feedback loops, is integrated and recognized by the thalamus in order to reach conscious awareness. Lateral geniculate nuclei are important structures within the thalamus that are likely highly involved in integrating processed information from throughout the cortex and reimagining this visual information within the 3D default space. We propose that other areas of the thalamus, such as the TRN, are also involved in the formation of visual and non-visual components of the 3D default space, though the specifics of which are beyond the scope of this paper. A study on pulvinar lesions found that patients with lesions in the anterior, posterior, or intermediate pulvinar had varying degrees of spatial and temporal deficits (Arend, Rafal, & Ward, 2008). Another study suggests that the pulvinar causes alpha-band synchronization between cortical areas, including the visual system (Saalmann, Pinsk, Wang, Li, & Kastner, 2012). For a detailed look at the TRN's possible role in consciousness see Min, 2010. Studies like these can give insights into the specific roles of different thalamic nuclei and their involvement in visual and non-visual consciousness. We propose that sensory information is processed and relayed by the contralateral thalamus and nuclei to the contralateral cortex and after higher processing this information is then integrated and merged with information from the other hemisphere into a seamless 3D space by the thalamus. This is apparent when examining the symptoms of contralateral neglect in which sensory information from the contralateral side to the parietal or thalamic lesion does not rise to conscious awareness.

This concept of a default 3D space can be better understood by examining contralateral neglect syndrome. Lesions in the right parietal cortex, which is composed of neurons that designate spatial location and orientation (Goldberg et al., 2006; Kusunoki & Goldberg, 2003), lead to neglect of the left visual space and left side of the body. These patients have no damage to their eyes or nerves yet they do not receive information from their left visual field and many do not receive information from the left side of their body. If contralateral neglect resulted exclusively in a visual processing defect, this would not explain the neglect of the left side of the body. If this syndrome affected only visual processing, patients would be able to receive sensory information from the left side of their body, but many do not. This CNS symptom gives us new insights into how the body schema may be formed within the mind. Many patients with CNS are not able to sense the contralateral side of their body because of their damaged parietal lobe. A healthy parietal lobe forms an internal grid or spatial map (Goldberg et al., 2006; Kusunoki & Goldberg, 2003) in which visual and other sensory information is organized. We propose that this sensory information remains unconscious because the partially processed or erroneous information from the parietal lobe is sent back to the thalamus and cannot be integrated with other sensory information in order to rise to conscious awareness.

When a person has a lesion in the parietal lobe, this grid of internal and external space fills in with sensory information from the right side of the body and right visual field but remains empty or damaged in areas of the spatial map for the left

side of the body and left visual field (Fig. 3). This visual and sensory information from the left side and left visual field is processed throughout the cortex but the damaged parietal lobe it is not able to project this information into this spatial grid. When this processed information gets feedback to the thalamus the sensory information from the left side is missing because it was not spatially oriented by the parietal lobe. This information is lost because it has no assigned source or location. This damaged spatial map is then integrated into the projected 3D default space by the thalamus so that the visual and sensory reimagining of the person and their surrounding environment within the mind, is missing the framework of the left side of the body and left visual field (Fig. 4.)

Studies have shown that visual stimuli that lead to significant brain activation throughout the brain can remain unconscious and unseen (Donner, Sagi, Bonneh, & Heeger, 2008; Libedinsky, Savage, & Livingstone, 2009; Scholvinck & Rees, 2010). Why some brain activity produces conscious perception and other activity does not is not well understood (Libedinsky & Livingstone, 2011). Processed information in the dorsal stream/parietal lobe is unconscious (Milner, 2012), it is not until further processing elsewhere in the brain that this information becomes conscious. We propose that the parietal lobe is essential for consciousness because it assigns spatial location (Goldberg et al., 2006; Kusunoki & Goldberg, 2003); however, information being processed in the parietal lobe, although essential for consciousness, is not yet conscious (Milner, 2012). The visual information does not become conscious until it is sent back to the thalamus and integrated with other information processed in parallel from throughout the cortex.

A study by Meador et al. found that the engrams of left-sided visuospatial memories of patients with CN are not destroyed but instead are not activated (Meador, Loring, Bowers, & Heilman, 1987). This supports the hypothesis that visuospatial information from the left side is present in the brain but does not become conscious and that the default 3D space may be involved in the creation and recollection of visual memories. Patients with CN have shown decreased cognitive abilities including poor episodic memory, working memory, and spatial abilities (Lee et al., 2008) suggesting that the default 3D space is involved in cognition and memory, though further studies are needed to examine its involvement.

Many areas of the brain, as well as afferent signaling from the body, are involved in consciousness. Our model expands on previous corticothalamic feedback models of consciousness and focuses on the role of visual and spatial processing in the parietal lobe and thalamus. We propose that unconscious, processed information from areas throughout the cortex, such as the parietal lobe, are then integrated within the thalamus producing a conscious 3D reimagining of space. This projection of space using processed visual and spatial information is within a default 3D space where outside space is reprojected within our bodies as inside space.

People see external visual space that is within their visual field, but this visual field is surrounded by external non-visual space and internal non-visual space within our bodies. This non-visual space consists of both conscious sensory input like sound, visceral sensations, and emotions but a large portion of this non-visual space is unconscious. The brain is constantly

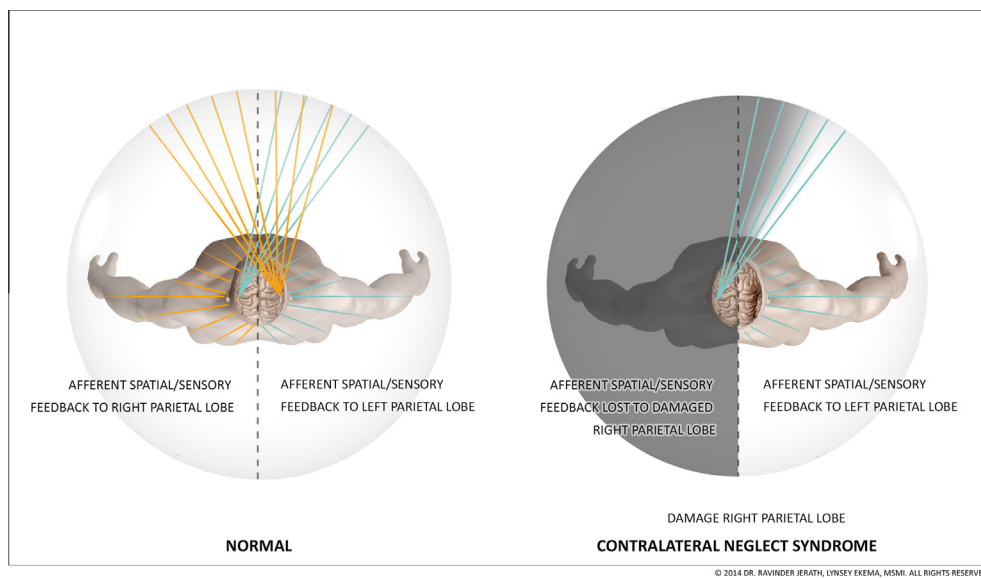


Fig. 3. Connections of the left and right parietal cortex: visual fields and body space: The figure depicts how the right parietal lobe, in a healthy individual, receives visual information from the left eye and sensory information from the left side of the body while the left parietal lobe receives sensory information from the right eye and right side of the body. The parietal lobes spatially map this information so that the mind can spatially locate stimuli. In contralateral neglect syndrome, when the right parietal lobe is damaged, information is fed to both parietal lobes, like in a healthy individual, but the intact left parietal lobe is able to spatially locate visual and sensory stimuli while the damaged right parietal lobe is not. The external visual information and internal sensory information sent to the damaged right parietal lobe does not become spatially oriented, like it does in a healthy individual, so this information never becomes a part of conscious awareness within the 3D default space. This results in a patient not being able to see or feel stimuli on their left side, even though their eyes, occipital lobe, and nerves are functioning normally. (Figure by Lynsey Ekema, MSML.)

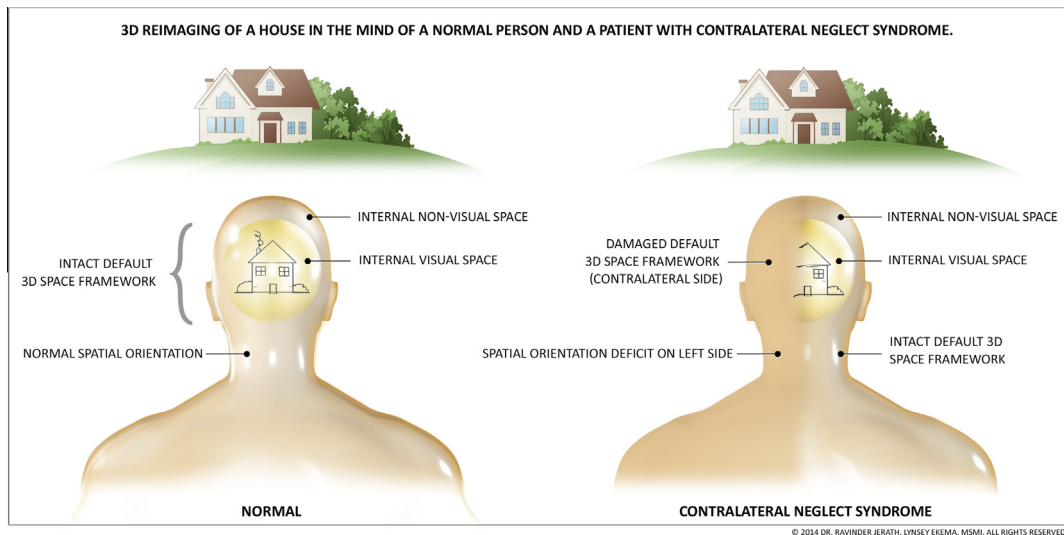


Fig. 4. 3D reimaging of a house in the mind of a healthy patient and a patient with contralateral neglect syndrome: In a healthy patient's brain, a house in their visual field is seen, processed, and reimaged in the 3D space in their mind. The right parietal lobe is intact so the entire framework of 3D space forms, including the reproduction of visual, non-visual, external, and internal space. In a patient with contralateral neglect syndrome, the left parietal lobe is intact while the right parietal lobe is damaged. The patient's eyes see the house within their visual field but the damaged parietal cortex is not able to locate the stimuli of the left visual field. The intact left parietal cortex is able to locate stimuli in the right visual field so when the house is reimaged by the thalamus, in the 3D space in their mind, the left visual field is missing. The patient does not consciously perceive the left visual field or the left side of their body and the left half of the default 3D space lacks a framework, boundaries, and spatial distribution. (Figure by Lynsey Ekema, MSMI.)

receiving sensory information from throughout the body that is spatially allocated by the parietal lobe and informs the rest of the brain of the boundaries of the body and the location of limbs within space. These non-visual internal and external spaces are not seen but they are seamlessly integrated into the spatial grid of the parietal lobe and the subsequent reimaging of external and internal visual space by the thalamus.

It is important to address the role of the olfactory system since it is the only sensory system that bypasses the thalamus. The olfactory bulb has a very similar structure and function to the thalamus and it has even been proposed that it could be considered an “olfactory thalamus” because it performs the preliminary roles of the thalamus for other sensory systems by processing and relaying olfactory information directly to the cortex (Kay & Sherman, 2007). Although the thalamus receives only a small amount of olfactory information directly via a few fibers connecting the olfactory bulb to the mediodorsal thalamus (Öngür & Price, 2000), it also receives processed olfactory signals indirectly from cortical regions that received the information via the olfactory bulb (Joseph L. Price, 1985; J. L. Price & Slotnick, 1983). In fact, patients with thalamic lesions have been shown to have impaired olfactory abilities, indicating the role of the thalamus in olfactory perception (Sela et al., 2009).

Trehub proposes a similar model in which there is a system of mechanisms of consciousness that create an internal 3D space that utilizes a neuronal center which represents the self within the brain's analog of 3D space (Trehub, 2007). His model differs from ours in that he proposes that visual information is projected in 3D space by a retinoid system of autaptic neurons that restimulate themselves. A 2D retinal image is projected onto these retinoid arrays, which creates a representation of 3D space in the brain (Trehub, 2007). This is a valuable model for how 3D space may be represented in the brain but it focuses on the retinas and the “retinoid system” without fully taking into account the extensive visual processing that occurs throughout the cortex and the fact that once processed, visual information is no longer exclusively retinal activity. Also, this model does not propose a specific neuronal center that creates this 3D space nor does it clearly define the parameters of the model.

Some researchers propose that the thalamus is not a likely structure responsible for consciousness because thalamic nuclei are small and therefore may not be able to support processes resulting in consciousness. However, each thalamic nuclei contains millions of neurons. For example, each thalamic reticular nucleus contains a million neurons with a mean density of $15,093 \pm 73$ neurons/mm³ (Zikopoulos & Barbas, 2006). We propose that the high number and density of neurons within thalamic nuclei, combined with the extensive processing performed by corticothalamic feedback loops makes the thalamus a realistic center for consciousness. Our proposed model also recognizes that the thalamus is not the only structure involved in consciousness. The entire brain is involved in consciousness, particularly corticothalamic feedback loops. The thalamus integrates processed information from throughout the cortex and reimages this within the 3D default matrix. Further supporting our model, anesthetics cause unconsciousness by blocking the brain from integrating information (Alkire, Hudetz, & Tononi, 2008). For example, thalamic nuclei activity was greatly reduced after the administration of halothane and isoflurane and activity of non-specific thalamic nuclei were even more reduced. This suggests that anesthesia blocks corticothalamic feedback loops and integration of processed information (White & Alkire, 2003) and may turn off

important processes in the thalamus that allow for consciousness to be achieved. Similar results were also seen after the administration of propofol (Fiset et al., 1999). Therefore, the thalamus is a realistic and primary candidate for the center of consciousness (Min, 2010).

6. Other conditions explained by our model of consciousness

Our model could explain the general mechanism behind CN, as well as other conditions like claustrophobia and motion sickness. Claustrophobia is an anxiety disorder in which the common factor is closed space (Ost, 2007). The cause of claustrophobia has been attributed to many different factors including conditioning, genetic predisposition (El-Kordi et al., 2013), and even amygdala size (Hayano et al., 2009). We propose that all of these factors may play a role in the underlying cause of claustrophobia, in addition to our model of consciousness, which helps to describe the mechanism behind this very common and debilitating disorder. The visual input to our consciousness sets the parameters of the internal non-visual space. For example, if our eyes see the horizon at the beach we feel free and unconstrained because the non-visual aspect of consciousness makes automatic adjustments to the visual field input. In another example, the visual input of a closed elevator causes the non-visual internal space to contract and makes the person feel enclosed. This situation may cause a person with claustrophobia to feel uncomfortable or anxious. Some people with claustrophobia even feel their level of anxiety rise when wearing tight-necked clothing (Ost, 2007). In addition, many people remove clothing trying to relieve symptoms during attacks. This may be due to the non-visual sensory information that influences the non-visual aspect of conscious 3D space. A study using the known biases of bisecting horizontal lines, found that people with larger peripersonal space had higher rates of claustrophobic fear than people with smaller peripersonal space (Lourenco, Longo, & Pathman, 2011), indicating a correlation between representations of space in the mind with claustrophobia.

Motion sickness is a condition in which there is a disparity between visually perceived movement and the sensory information from the vestibular systems (Eyeson-Annan, Peterken, Brown, & Atchison, 1996). Vestibular, visual, proprioceptive, and tactile inputs all contribute to our perception of spatial orientation (Pavard & Berthoz, 1977; Vidal, Amorim, McIntyre, & Berthoz, 2006) and motion sickness is likely due to erroneous information from the vestibular system being integrated with visual information in the 3D space in the mind or vice versa. This vestibular information is integrated within the non-visual space of the default 3D space, leading to the disparity between the non-visual vestibular information and visual information within the default 3D space. It has been proposed that motion sickness and the resulting nausea and emesis may have evolved as an adaptation against ingestion of neurotoxins that can also result in disparities between the visual and vestibular systems (Oman, 2012). This model of consciousness could also explain numerous other conditions and syndromes beyond CN, claustrophobia, and motion sickness, and processes such as how the brain stores visuospatial memories.

7. Conclusion

For some time, questions about consciousness and how the brain acts as the mind have been at the forefront of neuroscientific research. By examining contralateral neglect syndrome and pertinent literature, we have deduced a mechanism behind the processing of visual information and its role in consciousness. We propose that consciousness arises from integration of information from throughout the body and brain by the thalamus and that the thalamus reimages visual and other sensory information from throughout the cortex in a default 3D space in the mind. We have focused on the thalamus as a central hub and the roles of visual processing in consciousness, though there are many different aspects of consciousness, as well as the involvement of numerous areas of the brain. We propose that the thalamus generates a dynamic default 3D space by integrating processed information from corticothalamic feedback loops, creating an infrastructure that may form the basis of our consciousness. Further experimental evidence is needed to examine and support this hypothesis, the role of the thalamus, and to further elucidate the mechanism of consciousness.

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