

RECURRENT PROCESSING AND THE CONSCIOUSNESS

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Recurrent Processing and the Consciousness

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I hereby certify that all material in this final year project which is not my own work has been identified and that no work is included for which a degree has already been conferred on me.

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Abstract

Recurrent processing is the corticocortical activity that appears after the feedforward sweep of information processing in the brain. According to Victor Lamme, this process is directly connected to visual awareness. Our consciousness can be divided into phenomenal and reflective consciousness. The underlying process of phenomenal consciousness is suggested to be localized recurrent processing. Widespread recurrent processing to motor and frontal regions correlates with reflective consciousness. Recent electroencephalographic studies have shown visual awareness negativity correlating with localized recurrent processing in both a temporal and spatial aspect. If we accept that localized recurrent processing is consciousness, we get the controversial implications that we can be conscious of something without being able to introspect.

Keywords: recurrent processing, consciousness, visual awareness, visual processing, neural correlates of consciousness, visual awareness negativity

Table of Contents

Abstract	3
Introduction	5
Consciousness	7
Phenomenal Consciousness	8
Reflective Consciousness	10
Neural Substrate of Visual Processing	10
Functional or Anatomical Hierarchy	11
Temporal Hierarchy.....	13
Receptive Fields and Tuning Properties	14
Corticocortical Connections – Feedforward, Horizontal and Feedback.....	15
Neural Correlates of Consciousness.....	16
Four Stages of Neural Processing.....	17
Stage 1.....	18
Stage 2.....	18
Stage 3.....	18
Stage 4.....	19
The Neural Argument.....	19
Findings Supporting the Role of Recurrent Processing in Consciousness and Critique.....	21
Koivisto and Revonsuo’s Three Stages of Neural Processing	21
Stage 1: First positive (P1).....	23
Stage 2: Visual awareness negativity (VAN).	23
Stage 3: Late positivity (LP).	24
Absent or Interrupted Recurrent Processing.....	24
Critique	25
Global neuronal workspace theory.	26
Discussion	27
References	29

Introduction

Recurrent processing is a process in the brain which many scientists think have an important connection to visual consciousness (Bullier, 2001b; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Edelman, 1992; Lollo & Enns, 2000; Tononi & Koch, 2008). Lamme (2006; 2010a) argues that recurrent processing actually is consciousness and this brings controversy with it. This thesis will investigate recurrent processing, it will overview the central controversies that comes with a theory with recurrent processing connected to visual consciousness. The thesis will focus on Lamme's (Lamme, 2006; 2010a) theory on consciousness.

Consciousness and visual awareness are recent fields of study. Mental phenomena had no place in the field of science until the second half of the 1900th century (Baars, 2005; Searle, 2000). There are two main groups of theories of how we try to ontologically solve the mind body problem. The different types of dualistic theories hold that there are two different aspects of the world, the physical and the mental. The physical is all physical things and the mental is what forms our subjective experiences. The monistic theories define the world and mental phenomena as one single type of substance. Physicalism for example argues that everything, including the consciousness, can be explained with help from physics, chemistry and biology (Revonsuo, 2009; Searle, 2000).

The study of consciousness has emerged in science during the last ten years. The study of consciousness and visual awareness have grown and become possible because of new and more advanced imaging techniques such as functional magnetic resonance imaging (fMRI), electroencephalography (EEG) and magnetoencephalography (MEG). They have become more available to use in neuropsychological studies which have helped the field's accelerating progression (Lamme, 2000; Crick & Koch, 1998). Based on the new data from the imaging techniques, scientists have started to form testable hypothesis about the neural basis of

consciousness and visual awareness such as Recurrent Processing (Lamme, 2006), Global Workspace Theory (Baars, 2005), Neurobiological Theory (Koch, 1990), Information Integration Theory (Tononi, 2004), Thalamocortical Binding Theory (Linás, Ribary, Contreras, & Pedroarena, 1998), Microconsciousness-Theory (Zeki S. , 2003) and others.

Though there are many ways to attack the mind body problem this thesis will focus on the biological view of the problem (see e.g. Searle,2000). A first basic assumption will therefore be made and this is that the consciousness resides in the brain and nowhere else. It is a purely biological phenomenon and it should be studied as such (Searle, 2000), this is called *Biological Naturalism* (Searle, 2007). By doing this we can use biology and cognitive neuroscience to try to understand what in our brains enable us to have something as a consciousness (Crick & Koch, 1998). To define what our consciousness is, is a much harder problem. There are many philosophical viewpoints as well as biological, physical, computational or mathematical viewpoints (Revonsuo, 2006). Some attempts to define consciousness will be mentioned later in this thesis.

In this thesis, I will look at what role the neural process recurrent processing has in our visual consciousness. Visual consciousness and visual awareness is in many papers used synonymously (Lamme, 2010a; Koivisto & Revonsuo, 2010). In this thesis I will use the two terms in the same synonymous way. I will focus on Lamme's approach to visual consciousness, who argues that recurrent processing is the key neural ingredient for the consciousness (Lamme, 2006). I chose to focus on Lamme's theory because it has recently gotten lots of empirical support (Boehler, Schoenfeld, Heinze, & Hopf, 2008; Koivisto & Revonsuo, 2010; Railo, Koivisto, & Revonsuo, 2011; Fahrenfort, Scholte, & Lamme, 2008; Koivisto, Railo, Revonsuo, Vanni, & Salminen-Vaparanta, 2011; Supèr, Spekreijse, & Lamme, 2001) and because it has great explanatory power (Lamme, 2010a; 2006; 2004).

First there will be a discussion of different parts of the consciousness. Thereafter the neural substrate of visual processing will be introduced and explained. A correlation of the different neural processes in the brain to our subjective experience and our consciousness will be presented. In addition there will be a section with findings supporting the role of recurrent processing in the consciousness. Another section will mention some critique that has been given to Victor Lamme's theory that mainly focuses on the problem with introspection that comes with Lamme's theory. Finally I will discuss what the problems of accepting Lamme's theory we might encounter as well as suggest what further can be done in the science of consciousness.

This thesis will not address attention extensively though it is highly related to visual awareness and consciousness (Koivisto & Revonsuo, 2010; Lamme, 2004). This will be excluded because it is a big subject alone and this thesis focus on recurrent processing what function it has in visual consciousness. This thesis will briefly cover what is relevant for the neural correlates and findings related to consciousness, specifically related to visual consciousness. This is because it also is a big subject alone. Visual consciousness is the easiest part of consciousness to study at this time (Crick & Koch, 1998).

Consciousness

Defining consciousness is a really hard thing to do (Searle, 2000; Block, Flanagan, & Güzeldere, 1997; Honderich, 2005). Why are we conscious and how does it arise from our brain? We know how it is to be conscious but we have less understanding of it than any other thing in the world (Chalmers, 1993). If you ask someone the question: what is the consciousness? There will be many different answers and some might look like this: It is what we are aware of, it is what we see, feel, hear, smell and taste, and it is what we think of. This might be some of the answers a lay person would state. How it is to be something at all is one

way of approaching the problem (Nagel, 1997). Consciousness is originally no scientific concept but has its origin in folk psychology or everyday language (Revonsuo, 2006). Searle (2000) do not think it is hard to define it in folk psychological or common-sense terms: “Consciousness consists of inner, qualitative, subjective states and processes of sentience or awareness” (Searle, 2000, p. 559). One pragmatic definition is done by Dehaene et al. (2006) who abandons “consciousness” and instead use states of vigilance. The states can be seen as “a continuum of states which encompasses wakefulness, sleep, coma, anesthesia, etc.” (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006, p. 204). Crick and Koch (1998) don’t even bother defining it because in their opinion its time wasted which could be used studying the phenomena in the best possible way we can with what we have right now (Crick & Koch, 1998). Neuroscience and biology are great candidates for studying the consciousness and the biology of the mind (Revonsuo, 2006). By letting “...the arguments from neuroscience have a true say in the matter” (Lamme, 2006, p. 494) one can pragmatically study the consciousness and leave the philosophers to disagree about its definition as much as they want (Crick & Koch, 1998; Lamme, 2006).

In the same way as Revonsuo (2006) I will lay out a conceptual map of the consciousness in a way that is pragmatic to empirically study. It is not the only or the absolute correct division and classification of consciousness but it fills its practical purpose and it reflects in many ways what we experience in a first person perspective (Revonsuo, 2006). Ned Block (1995) does a similar division of consciousness.

Phenomenal Consciousness

Phenomenal consciousness is the first hand experience experienced by someone (Block, 1995; Farthing, 1992). It is “what it feels like” in contrast to what it does (Chalmers, 1993). The word phenomenal originates from psychology. Phenomena are psychological concepts describing “the immediate, undeniable facts of experience” (Revonsuo, 2006, s. 33).

Revonsuo (2006) divides phenomenal consciousness into presence, location, duration, intensity and quality. *Presence* is a part of my subjective experience right now in a temporal aspect. Right now I experience the soft tickle of a feather running down my palm of my hand and that is present right now in my experience. The *location* is that the experience occupies some location of my phenomenal sphere or my entire phenomenal sphere. The light from the moon is confined to a small dot in our phenomenal sphere. *Duration* means that an experience extends itself in time. Multiple discrete inputs can be experienced as one experience which is stretched out over a period of time. Experiences can vary in *intensity*. A light or sound may differ in strength, intensity, brightness or loudness. The *quality* of experiences is what separates an experience from others. The quality of the colour red is different from the quality of the colour blue which gives them different identities and makes them separable (Revonsuo, 2006). The concept of quality is comparable with qualia (Dennett, 1988).

Iconic memory can be used in a neuroscience perspective to understand phenomenality since it may be the closest thing we have to phenomenal experiences (Lamme, 2004). Ned Block (2007) is connecting the iconic memory and our phenomenal experiences though he uses phenomenal persistence instead of iconic since iconic is ambiguous in the sense that it can refer to what we can access and the phenomenality. With iconic memory tasks (Sligte, Scholte, & Lamme, 2008) the phenomenal consciousness can be separated from the reflective or access consciousness (Block, 2007; Lamme, 2010a) though this is very controversial and has gotten a lot of criticism, (see e.g. Lamme, 2010a; Block, 2007). Revonsuo (2006) criticise the concept of access consciousness stating that it “involves no necessary connection to subjective experience” (Revonsuo, 2006, s. 53). Block (1995; 1996; 2001; 2005; 2007) states that, in contrast with phenomenal consciousness, access consciousness is a form of reflective consciousness. Accessibility of the phenomenality is leading to controlling behaviour, our

acting out on it (Block, 1995; 1996). The phenomenal aspect of consciousness is accessed by the global workspace (Block, 2001; 2005; 2007).

Reflective Consciousness

After we have had a phenomenal experience, we can use introspection to reflect upon this experience (Chalmers, 1993). This is called reflective consciousness and can be compared to Block's access consciousness (Block, 2007) but see Revonsuo (2006) for critique. To be able to have any form of reflective consciousness, phenomenal consciousness is first necessary (Farthing, 1992). Without the phenomenal experience there is nothing to reflect upon (Revonsuo, 2006). A phenomenal experience can be two dots of different colour, e.g. blue and red, and your task is to tell them apart. First you look at the two dots and experience them phenomenally then you reflect upon what you see and for example make a verbal report of which one was red and which was blue. Thinking about the experience and forming a verbal report is called introspection (Chalmers, 1993). Verbal report is a possible outcome of reflecting upon the phenomenal experience we just had (Revonsuo, 2006).

Thus we separate the consciousness into two concepts (Block, 2005). Now let us take a look at the neural basis of these two concepts.

Neural Substrate of Visual Processing

To understand visual consciousness, an exploration of the neural substrate of visual processing is needed (Crick & Koch, 1998). The easiest way to start unravelling how visual consciousness work with *Biological Naturalism* (Searle, 2007) in mind, a look at the visual brain is in place.

First off, this section will explore the different areas of the visual brain, the stages of successive activation in an anatomical and temporal aspect, and then there will be a

description of what triggers some neurons to fire to certain stimuli and how it affects other neurons in the brain.

Functional or Anatomical Hierarchy

The functional hierarchy describes the different areas of visual processing. The hierarchical organization and processing of visual areas was first suggested by Hubel and Wiesel during the 1960s (as cited in Hubel, 1995). They got this idea from finding increasing complex tuning properties of neurons in the different visual cortical areas of the cat (Hubel, 1995). The macaque brain is very similar to the human brain and can be studied to better understand the human visual process. There are about 30 different areas for visual processing in the Macaque brain which of 25 is exclusively visual. The different areas are distinguished by the rate of visually responsive neurons in the areas and or the manifestation of larger inputs from known visual areas (Felleman & Essen, 1991).

Visual stimuli enter the eye and hit the retina with light. When the eye gets presented to a visual stimulus, for instance a dot of light that covers 3x3 degrees of our visual field, the rods and cones in our retina that are positioned reflecting the stimulus spatial position is activated by this stimulus – the cells on the retina that get hit by the light waves from the stimulus. The activity is then propagated through the cones and on to the ganglion cells in our retina and then continues to the optic nerve (Hubel, 1995). There are some intermediate steps with other cells which are beyond the scope of this essay. This surge of electrical and chemical activation then travels to the lateral geniculate bodies and then on to the cortex (Hubel, 1995). Cytochrome oxidase (CO) staining, an endogenous metabolic marker for neuronal activity (Wong-Riley, 1989), has revealed three different types of parallel pathways that run through the lateral geniculate nucleus (LGN). These are called magno- (M), parvo- (P) and koniocellular (K) pathways (Lamme & Roelfsema, 2000). These three different types of pathways or axon tracts have different conduction velocities. In the monkey the average

differences in velocities between the different axon types is significant. Magnocellular axons take 5.5 ms less than the Parvocellular axons to get the information sent. These measures are done between the retina and the cortex (Nowak & Bullier, 1997).

After Primary visual cortex (V1) they combine and then split into two new pathways (Figure 1). The magnocellular dominated pathway takes care of information dedicated to space, movement and action. This tract travels to the fourth layer, level Ca of the striate cortex and then to level B in the fourth layer. It continues to V3 and the thick layer of V2 and then on to medial temporal cortex (MT) and forth to parietal cortex. This path is referred to as the dorsal pathway. The ventral pathway largely consists of the parvo- and koniocellular connections. This pathway travels through the fourth layer of the striate cortex, level Cb, and then on to layer 4A through the blobs and interblobs and then on to V4 and temporal cortex. (Lamme & Roelfsema, 2000; Lamme, 2000; Maunsell & Essen, 1983).

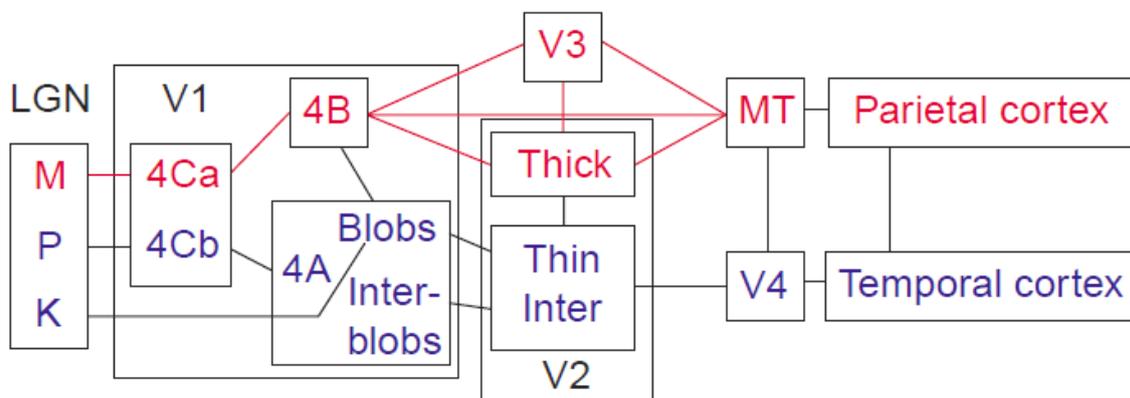


Figure 1. The path of the Magno- (M), Parvo- (P) and Koniocellular tracts through the dorsal (red; LGN, V1, V2, V3, MT and Parietal cortex) and ventral (blue; LGN, V1, V2, V4, Temporal cortex) streams. Modified from Lamme and Roelfsema (2000).

The dorsal and ventral streams are suggested to handle two different types of information (Lamme & Roelfsema, 2000). The dorsal stream travels through MT or V5 where MT comes from the medial temporal area of the owl monkey (Maunsell & Newsome, 1987)

whereas V5 or visual area 5 is the equivalent area in the human brain (Zeki, et al., 1991). The area MT is highly sensitive to direction of motion, stimulus speed of motion and stimulus orientation (Maunsell & Essen, 1983). This together with lesion studies suggest that the dorsal stream is specified in handling information related to spatial relationships (Maunsell & Newsome, 1987). The ventral stream is thought to be handling information about objects. Several lesion studies have shown that damage to temporal cortex impair object recognition and face recognition (Maunsell & Newsome, 1987).

Temporal Hierarchy

Next to this anatomical or functional hierarchy is the temporal hierarchy. The temporal hierarchy is determined by response latencies from visual stimulation onset to activation of different visual areas of the brain. The activation visual areas seen from a temporal perspective is different from the anatomical in the way that some of the higher order anatomical areas are activated earlier in time than lower order areas (Lamme, 2000). As early as in the ganglion cells in our retina there is a difference in latencies between magno- and parvocellular cells. The magnocellular cells are activated about 10-20ms before the parvocellular cells. This latency is still present in the lateral geniculate nucleus as well as in V1. As mentioned earlier in the anatomical and functional hierarchy, the parvo- and magnocellular axons reside in different levels of the layer 4 in V1 so there will be a difference in latency of activation (Nowak & Bullier, 1997; Schmolesky, et al., 1998).

The earliest activation after the geniculate cortex is in primary visual cortex. It can be activated as early as 35ms after stimulus onset. Almost at the same time as the primary visual cortex (35ms), the frontal eye field (FEF) (43ms) and middle temporal cortex (MT) (39ms) is activated (Lamme & Roelfsema, 2000). This is an example of what separates the functional or anatomical hierarchy from the temporal hierarchy (Lamme, 2000; Lamme & Roelfsema, 2000). Further up in the temporal hierarchy are the areas V2 (54ms), V3 (50ms) and V4

(61ms). At the top of the ventral stream in the temporal hierarchy, we have the temporal lobe with its substructures TE1 (86ms) and TE2 (83ms) (Lamme & Roelfsema, 2000). The top of the dorsal stream is harder to define but to get an idea of the high levels of the dorsal stream, the orbitofrontal gyrus (OrbFr) and primary motor cortex (M1) has activity around 80-85ms (Lamme & Roelfsema, 2000). It takes about 10ms for areas that are directly connected to send information to each other. For example it takes 10ms for information from V1 to reach V2 and the same between V1 and MT (Nowak & Bullier, 1997).

The two perspectives (anatomical or functional and the temporal) of visual information processing during the initial stage of processing can be seen as the feedforward sweep. It is the initial processing of a visual stimulus during the first 100ms after stimulus onset (Lamme, 2000).

Receptive Fields and Tuning Properties

To define classical receptive field we can think of a small area in the primary visual cortex. This specific area can only be activated by a single stimulus such as a bar or a spot (Maunsell & Newsome, 1987). So when light from the 3x3 degrees of our visual field hits the rods and cones in our retina, they send information to the ganglion cells and so on all the way to our cortex. The cells in our cortex that is activated by this speck of light, or the neurons which are tuned to this specific stimulus, when they get activated, it is because they are the classical receptive field for that stimulus (Lamme & Roelfsema, 2000). The higher we get in the anatomical hierarchy, the more specific is the tuning of cells (Lamme & Roelfsema, 2000) thus they have larger receptive fields (i.e. there are more neurons that combine their activation and connections to make a single neuron to fire with all these cells using activation and inhibition) (Hubel, 1995; Lamme & Spekreijse, 2000).

If we then try to light a flashlight into the eye, we would not get as much of a response as we maybe think that we would get. This is because of the inhibitory effects that cells have when the stimulus is not in the centre of its classical receptive field (Hubel, 1995). These inhibitory surrounds or contextual modulations have been further investigated by Lamme (1995) looking at figure-ground segregation. In a study they had wake macaque monkeys who looked at a screen with random dots or random bars. The random bars were all in the same direction. In the dot display, a figure of moving dots appeared in the shape of a square. In the random bars display, a figure of differently oriented bars appeared in a shape of a square. The activity of the neurons in the primary visual cortex with receptive fields located where the figures and where the background was located, were recorded. The results were that cells with receptive fields on the figure had higher activity with a latency of 30-40ms than the surrounding cells. This elevated activity is suggested to be because of surround inhibition or contextual modulation (Lamme, 1995; Lamme & Spekreijse, 2000). These surround inhibitions have been seen in V2 connected to illusory contours as well as in V4 when we distinguish colour constancy (Maunsell & Newsome, 1987; Bullier, 2001b).

Corticocortical Connections – Feedforward, Horizontal and Feedback

There are different types of connections between structures in our brain which send information in different directions. Those who travel up in the functional and anatomical hierarchy are what constitute the feedforward sweep of information. The connections that go from higher to lower is called feedback connections and the ones going within cortical regions is called horizontal connections (Lamme, Supèr, & Spekreijse, 1998). During the feedforward sweep of activation, the neurons tuning is decided by their classical receptive fields (Lamme & Spekreijse, 2000). The cells tunings are not static in the sense that they have different tuning properties and this is affected by the temporal aspect of activity i.e. at longer latencies cells exhibit different tunings (Lamme, 2000). The feedback and horizontal connections are

suggested to be responsible for these modulated tuning properties (Lamme & Spekreijse, 2000; Bullier, 2001b; 2001a). Together, the horizontal and the feedback connections are what we call recurrent processing (Lamme, 2010a). It is the activity that can travel back from the feedforward sweep and between areas which can change how the neurons respond instead of their classical tuning. This recurrent processing alters the way in which visual areas process information and make processing more complex which can give rise to our visual experience (Lamme, 2000; 2006). Recurrent processing is the most important neural aspect of Lamme's (2006) theory of visual consciousness.

Different visual areas in the brain form corresponding topographical maps of the visual field. The different maps in the different areas of the brain have increased connectivity and it is between these maps the re-entrant (Edelman, 1992) or recurrent processing is seen. Multiple maps then together send re-entrant outputs which together form a higher-order structure called global mapping which control motor areas to guide motor outputs (Edelman, 1992).

Neural Correlates of Consciousness

This thesis has presented how our consciousness can be divided in what the different parts of experience we might have. It has explored the neural substrate of vision and the different properties our visual system have in terms of connections and flows of information. Now the thesis will present how the different activities in the brain can be connected with what we experience. In other terms what are the neural correlates of consciousness. An interesting question is if there are any specific neural correlates of consciousness. Is there actually any part or parts of the brain which together brings about our consciousness by sheer activity?

To sustain a general conscious state, modulations of frontal and parietal cortical networks through thalamic nuclei is essential (Railo, Koivisto, & Revonsuo, 2011).

Activation of any visual areas alone is not sufficient nor necessary to generate a visually phenomenal awareness (Rees, 2007). What brain areas are then necessary and sufficient to generate conscious experience? What is the minimal activity that generates visual experience? (Tononi & Koch, 2008; Crick & Koch, 1998; 2003). It seems to be the types of connections that integrate information from several areas such as recurrent processing instead of activity in individual areas that give rise to conscious visual perception (Lamme, 2010a).

Since there is no area alone that seem to account for our consciousness, the neural correlates of visual consciousness cannot be localized somewhere in the brain. This means that properties of receptive field cells generated by feedforward processing do not generate visual awareness. For example the activation of cells tuned to motion does not alone give rise to conscious sensation of movement and face selective cells do not when activated generate face perception (Lamme, 2000).

Feedforward activations do not themselves bring forth visual perception (Lamme, 2010a). Some studies have correlated early feedforward activity to consciousness. Railo, Koivisto, and Revonsuo (2011) explain these findings to be related to attention. Early event related potentials (ERP) waves related to the feedforward sweep are known to be modulated by attention (Railo, Koivisto, & Revonsuo, 2011).

Four Stages of Neural Processing

Lamme (2010) distinguishes four different but gradual stages of neural processing consisting of feedforward and recurrent processing. Their depth of processing connected with attention and level of conscious status separate them from each other (Lamme, 2010a).

Stage 1.

Stage one is the shallowest form of unconscious processing. It appears during the feedforward sweep when a stimulus is unattended and masked (Lamme, 2010a). For example if a person should be exposed to a first stimulus with words and then gets to see a second image with something else. If the second image is presented 40 ms after the first, it will work as a mask and make the first image invisible (Lamme & Roelfsema, 2000). The words that were not attended during the first picture will be masked and this fits to this first stage. This stage of processing does not propagate high enough in the ventral stream to reach word-form selective areas (Lamme, 2010a).

Stage 2.

Stage two consists of a deeper feedforward processing. This stage is invisible and unconscious. An attended but masked stimulus has the capability of entering the second stage of processing (Lamme, 2010a). For example an image of a face which get masked by a second stimulus. The face gets processed all the way up to IT but will not be visible. However, it can influence behaviour in the form of unconscious priming (Lamme, 2010a).

Stage 3.

Stage three is the first stage we can see recurrent or re-entrant processing appear, though it is localized and superficial. This third stage of processing is not attended. It is neglected as in change blindness, neglect, attentional blink or inattention blindness (Lamme, 2010a). In these conditions, subjects do not report having a conscious visual experience of the stimulus (Koivisto & Revonsuo, 2010; Lamme, 2006; Scholte, Witteveen, Spekreijse, & Lamme, 2006).

Stage 4.

In stage four, widespread or deep recurrent processing is seen. The recurrent processing in this stage reaches from low to high hierarchical areas with executive areas at the top. When a stimulus is attended and is not disrupted within critical time, this type of processing can come about. The fourth stage of processing can be equated with reaching Baars (2005) global workspace (Lamme, 2010a; Baars, 2005).

The Neural Argument

Lamme (2010a) argues that the feedforward sweep is unconscious, localized recurrent processing is conscious but only phenomenally conscious and that global or widespread recurrent processing is allowing us to have reflective consciousness e.g. verbal report.

Since the feedforward sweep alone is insufficient to produce phenomenal experience, stage 1 and 2 can be excluded from what is sufficient for conscious processing. Stage 4 has recurrent processing which spans the whole brain. It reaches frontal areas and accounts for report and is sufficient for conscious perception and other higher cognitive functions such as report. At this stage, residues of neural processing correspond to working memory. Stage 3 has recurrent processing but do not reach frontal areas and lack report. During this stage of processing residual neural activity correspond to iconic memory which leaves a carbon copy of our visual scene which corresponds to our phenomenal experience. Since stage 3 has recurrent processing and only differs from stage 4 in reaching higher areas, is it phenomenal? This is the big controversial question (Lamme, 2010a). If stage 3 actually is phenomenal and thus conscious, it means that humans and animals with consciousness comparable to humans' consciousness can be visually conscious of stimuli without being able to report about it. This is controversial in the sense that it is counterintuitive to think of being conscious without being able to report about it. It does not seem to be in that way when we introspect about it, how I can be conscious of something without knowing it myself. According to Lamme

(2010a), introspection does not alone show what is conscious but recurrent processing is a great candidate to do so.

According to Lamme (2010a), it is fairly well established that recurrent processing is necessary for visual awareness. Is it recurrent processing that is the key neural ingredient that gives Stage 4 phenomenality or is it the frontal activation? It is further known that feedforward activation of face selective areas only categorize a visual stimuli as a face or not but the information from V1 and lower areas has to be integrated to see the face in a context i.e. in colour, motion, related to other objects and the different unique properties of the face (Lamme, 2010a).

Recurrent processing further satisfies the criteria by having enough information integration, but not too high e.g. seizures are known to generate synchronous activity which is too high and non-specific to produce phenomenality. Feedforward networks generate low integrated information which further supports stage 1 and 2 being insufficient in generating phenomenality thus supporting recurrent processing as an ingredient in consciousness (Lamme, 2010a).

In addition, there is another major difference between the two types of processing. During recurrent processing both pre- and postsynaptic neurons are active at the same time. This is satisfactory for the Hebb rule which leads to synaptic plasticity and this is a key neural process in learning and memory (Lamme, 2006; 2010a).

These neural arguments make no difference between stage 3 and 4 which both have recurrent processing. The only difference is the wider range of activity reaching frontal areas responsible for cognitive control. Lamme (2010a) dissociates consciousness from cognitive control and attention and thus stating that we in fact are conscious during stage 3. According to Koivisto and Revonsuo (2010) phenomenal awareness is relatively independent from

nonspatial attention and reflective consciousness is dependent on all forms of attention.

Report and consciousness are different things and “linking visual phenomenality to access and report gives the whole notion of consciousness a poor ontological status” (Lamme, 2010a, p. 219). According to Lamme (2006) “We could even *define* consciousness as recurrent processing” (Lamme, 2006, p. 499). Report or access to the phenomenality appears when the processing reaches stage 4 and becomes widespread or globally accessible for higher cognitive areas to enable us to report it through motor functions such as speech or reflection (Lamme, 2010a).

Findings Supporting the Role of Recurrent Processing in Consciousness and Critique

Koivisto and Revonsuo’s Three Stages of Neural Processing

EEG research of the timing of the neural processing related to our visual awareness has been done for a long time. When EEG is used to correlate neural activity to psychological events, one looks at the event related potentials (ERP) (Koivisto & Revonsuo, 2010). With ERPs, we are able to look at the brain’s average electrical response to some specific sensory event. This technique has great temporal resolution. It is so fine that we can separate neural events by milliseconds to see the activity reflecting a stimulus that appear in the visual field (Railo, Koivisto, & Revonsuo, 2011). To relate ERP to visual awareness one has to manipulate visual awareness and compare visually aware neural activity to the activity which does not reach awareness. There are several methods in which this can be accomplished. Koivisto and Revonsuo (2010) have done a review of the work published on visual awareness and ERP done the last 10 years. The methods used to manipulate visual awareness in Koivisto and Revonsuo’s (2010) review was *masking, reduced contrast stimuli, attentional blink, change blindness* and *bistable perception*.

In *masking*, a stimulus is presented with a mask before (forward mask) or after (backward mask) to render the stimulus invisible to the subject. The mask needs to be presented with short stimulus-onset asynchrony (SOA) to have full effect in masking the stimulus. When using *reduced-contrast stimuli*, the subject is exposed to a stimulus near the threshold for the stimulus to reach visual awareness. When trying to identify a second target after a first amongst a rapid flow of non-targets, subjects do not see the second target if the two targets are presented with a SOA of 200-500 ms. It is called *attentional blink* when the subject fails to see the second target. *Change blindness* occurs when we do not detect changes between two images presented in succession. *Bistable perception* can be achieved by viewing an image which do not change but give rise to different content of our visual awareness. Binocular rivalry is a type of bistable perception where different images are exposed to each eye. Only one of the images reaches awareness at a time (Koivisto & Revonsuo, 2010).

Koivisto and Revonsuo (2010) distinguish between three different stages of visual processing (Figure 2), the first positive component after about 100 ms related to attention, visual awareness negativity (VAN) which consist of the negative components around 200 ms and the late positive (LP) or P3 component which usually appears at around 300-400 ms after

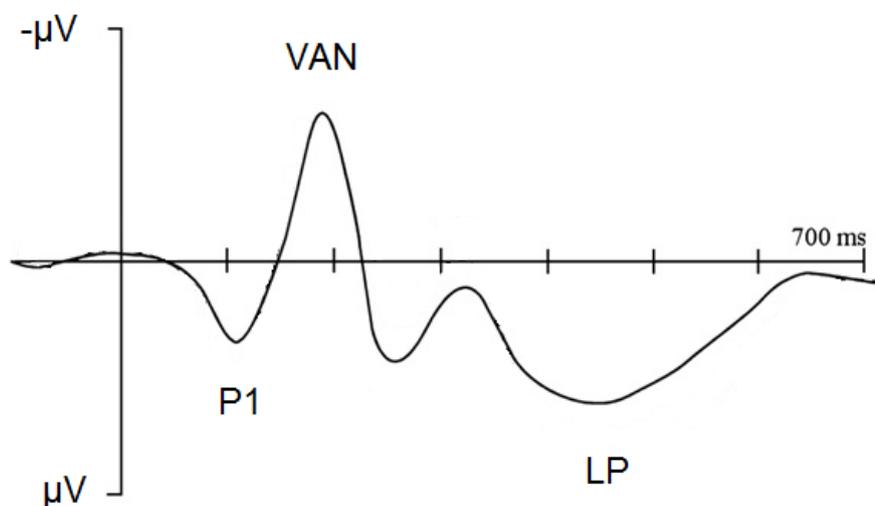


Figure 2. The first positive P1, visual awareness negativity (VAN) and late positivity (LP) pointed out on a typical ERP waveform. Modified from Railo, Koivisto and Revonsuo (2011).

stimulus onset (Koivisto & Revonsuo, 2010).

Stage 1: First positive (P1).

The first positive or P1 component of visual processing has higher amplitude when visually aware stimuli are processed. This means that sensory processing is enhanced for stimuli reaching awareness (Koivisto & Revonsuo, 2010; Railo, Koivisto, & Revonsuo, 2011). This can be explained by attentional selection. Stimuli selected by attention are reflected in amplified P1 components and thus can be dissociated with visual awareness *per se* (Koivisto & Revonsuo, 2010; Railo, Koivisto, & Revonsuo, 2011).

The first positive component corresponds roughly with Stage 1 and 2 of Lamme's model of processing (Lamme, 2010b) hence supporting Lamme's theory.

Stage 2: Visual awareness negativity (VAN).

Most consistently, VAN emerges at 200 ms after a stimulus has been presented. It can though start as early as at 100 ms and remain up to 300-460 ms after stimulus onset. The activity appears in the occipito-temporal area of the brain found out by help of low resolution electromagnetic topography (Koivisto & Revonsuo, 2010). VAN has been proposed to be the ERP neural correlate of visual awareness because of its consistent appearance in the visual awareness manipulating methods used in fining the temporal aspect of visual awareness (Koivisto & Revonsuo, 2010; Railo, Koivisto, & Revonsuo, 2011).

VAN fits especially well with Lamme's theory. The ventral localization of the VAN (Koivisto & Revonsuo, 2010) corresponds to Lamme's (2010) view of where the localized recurrent processing appears which brings forth visual consciousness or phenomenal consciousness (Lamme, 2010a). VAN also appears around 200 ms (Koivisto & Revonsuo, 2010) which is when localized recurrent processing is seen (Lamme, 2010a). Recurrent processing has been proposed to be the activity causing VAN (Railo, Koivisto, & Revonsuo,

2011) thus further supporting recurrent processing's role in visual consciousness in Lamme's theory (Lamme, 2006).

Stage 3: Late positivity (LP).

After VAN, LP usually appears but not necessarily. LP is typically seen in the 300-400 ms time window thus starting directly after VAN has spiked. Its activity is positioned at parieto-central sites of the brain. LP is suggested to correspond to activity reflecting post conscious cognitive functions and thus do not reflect phenomenal consciousness (Koivisto & Revonsuo, 2010). This dissociation is suggested because of visually perceived stimuli which evoked VAN but not LP (Koivisto & Revonsuo, 2010; 2008).

LP fits well with the concept of reflective consciousness. LP appears in the P3 window of a visually processed stimulus. This corresponds to the timing of updating of working memory (Koivisto & Revonsuo, 2010). LP dissociation from VAN does accord well with Lamme's theory which separates reflective cognitive operations from phenomenal experiences (Koivisto & Revonsuo, 2010; Lamme, 2010a).

Absent or Interrupted Recurrent Processing

Experiments on monkeys have shown that when they do not report seeing a stimulus there is concurrent absence of contextual modulation (Supèr, Spekreijse, & Lamme, 2001). Contextual modulation is related to figure ground segregation (Lamme, 1995) which is a process proposed to be constituted of recurrent processing (Lamme, 2000). In contrast to not seen stimuli, when the monkey sees the stimulus it comes with accompanying modulations. There are though stimuli with low saliency which don't get reported seen by the monkey but still show weak contextual modulation (Supèr, Spekreijse, & Lamme, 2001).

Another monkey experiment was conducted where the monkey was anaesthetized and exposed to visual figure-ground stimuli compared to awake. When the monkey was anaesthetized there was no contextual modulation (Lamme, Zipser, & Spekreijse, 1998).

These findings support the recurrent processing theory and the role of recurrent processing in visual consciousness. The low saliency stimulus which gets processed but not reported (Supèr, Spekreijse, & Lamme, 2001) fits well with localized recurrent processing not reaching motor areas for report (Lamme, 2006).

Several Transcranial Magnetic Stimulation (TMS) experiments have been conducted where the feedforward surge of activity as well as the recurrent interactions have been suppressed during visual stimulation rendering the stimulus invisible (Lamme, 2000; Koivisto, Railo, Revonsuo, Vanni, & Salminen-Vaparanta, 2011). When a visual stimulus' feedforward sweep gets interrupted in V1 at around 0-50 ms after stimulus onset, it gets suppressed in contrast to when TMS is applied between 50 and 80 ms the impairment is less. TMS suppression at 80 to 150 ms impairs visibility the most (Lamme, 2000).

This further supports the recurrent interactions role after the feedforward sweeps in producing conscious perception (Lamme, 2000).

Critique

According to Caplovitz, Arcaro and Kastner (2010) we do not see the world as it is but rather a best guess of what it is. This is in contrast to what Lamme propose iconic memory reflects (Lamme, 2010a). Additionally they argue that Instead of searching for how our brain creates consciousness of a visual stimulus we should examine how our continuous conscious experience change (Caplovitz, Arcaro, & Kastner, 2010).

Holding on to introspection is something that is common in the critique against Lamme's theory. Some define consciousness as being able to report about it. To be able to

have qualia it requires the quale to be introspectively accessible (Ibáñez & Bekinschtein, 2010) thus directly contradicts Lamme's attempt to discern phenomenality and report. Overgaard (2010) states that neural arguments fail to disregard introspection. To be able to know if someone is conscious of something we have to use introspection in the first place. Introspection is a valid indicator of consciousness and its absence (Shanahan, 2010). Ibáñez & Bekinschtein (2010) further criticize Lamme's theory because it does not explain qualia but properties of visual integration.

According to Shanahan (2010) Lamme has misunderstood the Global Workspace Theory. Widespread activity need not only go to frontal areas for report to bring forth consciousness but it needs to go everywhere (Shanahan, 2010).

Global neuronal workspace theory.

An opposing theory that does not centralize on recurrent processing is the global neuronal workspace theory (GNWT) (Baars, 2005; Dehaene & Naccache, 2001; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). The main idea of the theory is that separate modules or brain functions do process simultaneously and parallel to form a global workspace. The workspace enables the *fleeting memory* which incorporates information from all the different areas such as the different sensory processors. The information is integrated to a whole – the spotlight or theater of our mind (Baars, 2005). GNWT focuses on the ability to report what is conscious and accompanying activation of the higher associative cortices, parietal, prefrontal and anterior cingulate areas (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). Dehaene, Changeux, Naccache, Sackur, and Sergent (2006) distinguish between three different stages of processing, subliminal, preconscious and conscious processing. The subliminal stage can be divided into attended and unattended subliminal processing thus resulting in four stages. These four stages underlying neural processing is directly comparable to Lamme's (2010a) four stages of processing earlier explored in this

paper. Dehaene et al. (2006) only ascribe stage 4 to be conscious whereas Lamme (2010a) ascribe both stage 3 and for to be conscious. Dehaene et al. (2006) thus equates the ability to report and consciousness. This is in opposition to Lamme (2010a).

Discussion

This thesis has examined the role of recurrent processing in visual consciousness. No absolute definition of consciousness has been made but rather a conceptual map. This is because it is pragmatic and easy to empirically study. *Phenomenal* and *reflective* consciousness has been explained and correlated with processes or stages of processing in the brain. Lamme (2010a) proposes that there are four stages of processing. Stage 1 and stage 2 is made up of feedforward processing in different degrees which are unconscious. Stage 3 and stage 4 consist of localized and widespread recurrent processing respectively. What is different between the two stages is that stage 4 has recurrent processes reaching motor areas and thus enables report. Lamme (2010a) thus argues that we are phenomenally conscious of stage 3 but verbal report of the phenomenality is not possible.

There is substantial empirical support in favour of this theory. Recent electroencephalography (EEG) studies show visual awareness negativity (VAN) which correspond both spatially and temporally with localized recurrent processing (Koivisto & Revonsuo, 2010). VAN is proposed to be the ERP correlate of visual consciousness (Koivisto & Revonsuo, 2010; Railo, Koivisto, & Revonsuo, 2011). There are also TMS studies that interrupt recurrent processing which makes stimuli invisible (Koivisto, Railo, Revonsuo, Vanni, & Salminen-Vaparanta, 2011; Lamme, 2000) thus supporting Lamme's theory.

Some criticism has been made against Lamme's theory, mainly the problem of introspection and verbal report (Ibáñez & Bekinschtein, 2010; Overgaard, 2010; Shanahan, 2010; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). According to Dehaene et al.

(2006) and GNWT, we are not conscious of the localized recurrent processing. Conscious sensations of what we did see do not appear until the information has spread to higher order areas such as frontal regions. The information need to spread globally to reach consciousness. If we were to accept Lamme's neural argument and define phenomenal or visual consciousness as localized recurrent processing, this would infer that we could be visually conscious of certain stimuli without "knowing" it. Introspectively, we usually recognize being conscious of something by either introspecting or verbally reporting it to others or to ourselves by means of inner speech. So if we are to accept Lamme's theory this intuitive way of categorizing a conscious sensation by verbal report or inner speech, it would be insufficient to identify our own visual awareness. We could lie down in a functional resonance imaging (fMRI) machine or use EEG to see that we actually were conscious of something we did not know. According to Lamme we simply forgot our conscious experience since we cannot equate consciousness with working memory (Lamme, 2006).

What should be further studied is what probably everyone studying the neural correlates of consciousness along with all philosophers of consciousness thinks: how a process in the brain such as recurrent processing (Lamme, 2010a) can lead to a phenomenal experience or qualia. This is the "hard problem" (Chalmers, 1995) and it is probably too early to solve at the state of consciousness research today.

Recurrent processing should be examined and correlated to other conscious sensations such as olfactory, gustatory or auditory experience.

As Lamme (2010a) mentions, it should be investigated in bistable perception whether recurrent processing cease in the suppressed percept. This would give strong support to recurrent processing and its role in visual consciousness.

References

- Baars, B. J. (2005). Global workspace theory of consciousness: Toward a cognitive neuroscience of human experience. *Progress in Brain Research*, 150, 45-54.
- Block, N. (1995). On a confusion about a function of consciousness. *Behavioral and brain sciences*, 18(2), 227-287.
- Block, N. (1996). How can we find the neural correlate of consciousness? *Trends in Neuroscience*, 19, 456-459.
- Block, N. (2001). Paradox and cross purposes in recent work on consciousness. *Cognition*, 79, 197-219.
- Block, N. (2005). Two neural correlates of consciousness. *TRENDS in Cognitive Sciences*, 9(2), 46-52.
- Block, N. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. *Behavioral and brain sciences*, 30, 481-548.
- Block, N., Flanagan, O., & Güzeldere, G. (1997). *The nature of consciousness*. Massachusetts: The MIT Press.
- Boehler, C. N., Schoenfeld, M. A., Heinze, H.-J., & Hopf, a. J.-M. (2008). Rapid recurrent processing gates awareness in primary visual cortex. *PNAS*, 105(25), 8742–8747.
- Bullier, J. (2001a). Feedback connections and conscious vision. *TRENDS in Cognitive Sciences*, 5(9), 369-370.
- Bullier, J. (2001b). Integrated model of visual processing. *Brain Research Reviews*, 36, 96-107.

- Caplovitz, G. P., Arcaro, M. J., & Kastner, S. (2010). Stage 3 and what we see. *Cognitive Neuroscience*, 1(3), 220-222.
- Chalmers, D. J. (1993). Towards a theory of consciousness. *University of Indiana Ph.D. thesis*.
- Chalmers, D. J. (1995). Facing Up to the Problem of Consciousness. *Journal of Consciousness Studies*, 2(3), 200-219.
- Crick, F., & Koch, C. (1998). Consciousness and neuroscience. *Cerebral Cortex*, 8, 97–107.
- Crick, F., & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, 6(2), 119-126.
- Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition*, 79, 1-37.
- Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *TRENDS in Cognitive Sciences*, 10(5), 204-211.
- Dennett, D. C. (1988). Quining Qualia. In A. J. Marcel, & E. Bisiach (Eds.), *Consciousness in contemporary science* (pp. 381-414). New York: Oxford University Press.
- Edelman, G. M. (1992). *Bright air, brilliant fire: On the matter of the mind*. New York: BasicBooks.
- Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. (2008). The spatiotemporal profile of cortical processing leading up to visual perception. *Journal of Vision*, 8(1), 1-12.
- Farthing, G. W. (1992). *The psychology of consciousness*. Upper Saddle River, NJ: Prentice Hall.

- Felleman, D. J., & Essen, D. C. (1991). Distributed Hierarchical Processing in the Primate Cerebral Cortex. *Cerebral Cortex*, 1, 1-47.
- Honderich, T. (2005). *The oxford companion to philosophy*. New York: Oxford University Press.
- Hubel, D. H. (1995). *Eye, brain, and vision* (Vol. 22). Scientific American Library Series.
- Ibáñez, A., & Bekinschtein, T. (2010). Explaining seeing? Disentangling qualia from perceptual organization. *Cognitive Neuroscience*, 1(3), 223-224.
- Koch, F. C. (1990). Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences*, 2, 263-275.
- Koivisto, M., & Revonsuo, A. (2008). Comparison of event-related potentials in attentional blink and repetition blindness. *Brain Research*, 1189, 115-126.
- Koivisto, M., & Revonsuo, A. (2010). Event-related brain potential correlates of visual awareness. *Neuroscience and Biobehavioral Reviews*, 34(6), 922-934.
- Koivisto, M., Railo, H., Revonsuo, A., Vanni, S., & Salminen-Vaparanta, N. (2011). Recurrent processing in V1/V2 contributes to categorization of natural scenes. *The Journal of Neuroscience*, 31(7), 2488–2492.
- Lamme, V. A. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. *The Journal of Neuroscience*, 15(2), 1605-1615.
- Lamme, V. A. (2000). Neural mechanisms of visual awareness: A linking proposition. *Brain and Mind*, 1, 385-406.
- Lamme, V. A. (2004). Separate neural definitions of visual consciousness and visual attention; a case for phenomenal awareness. *Neural Networks*, 17, 861-872.

- Lamme, V. A. (2006). Towards a true neural stance on consciousness. *TRENDS in Cognitive Sciences*, 10(11), 494-501.
- Lamme, V. A. (2010a). How neuroscience will change our view on consciousness. *Cognitive Neuroscience*, 1(3), 204-220.
- Lamme, V. A. (2010b). What introspection has to offer, and where its limits lie. *Cognitive Neuroscience*, 1(3), 232-235.
- Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *TRENDS in neuroscience*, 23, 571-579.
- Lamme, V. A., & Spekreijse, H. (2000). Modulations of primary visual cortex activity representing attentive and conscious scene perception. *Frontiers in Bioscience*, 5, 232-243.
- Lamme, V. A., Supèr, H., & Spekreijse, H. (1998). Feedforward, horizontal, and feedback processing in the visual cortex. *Current Opinion in Neurobiology*, 8, 529-535.
- Lamme, V. A., Zipser, K., & Spekreijse, H. (1998). Figure-ground activity in primary visual cortex is suppressed by anesthesia. *PNAS*, 95, 3263–3268.
- Llinás, R., Ribary, U., Contreras, D., & Pedroarena, C. (1998). The neuronal basis for consciousness. *Philosophical Transactions of the Royal Society of London (Series B, Biological Sciences)*, 353, 1841-1849.
- Lollo, V. D., & Enns, H. T. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General*, 129(4), 481-507.

- Maunsell, J. H., & Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed and orientation. *Journal of Neurophysiology*, *49*(5), 1127-1147.
- Maunsell, J. H., & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. *Annual Reviews Neuroscience*, *10*, 363-401.
- Nagel, T. (1997). What is it like to be a bat. In N. Block, O. Flanagan, & G. Güzeldere (Eds.), *The nature of consciousness* (pp. 519-528). Massachusetts: The MIT Press.
- Nowak, L. G., & Bullier, J. (1997). The timing of information transfer in the visual system. In K. S. Rockland, J. H. Kaas, & A. Peters (Eds.), *Cerebral Cortex: Extrastriate Cortex in Primates* (Vol. 12, pp. 205-241). New York: Plenum Press.
- Overgaard, M. (2010). How consciousness will change our view on neuroscience. *Cognitive Neuroscience*, *1*(3), 224-225.
- Railo, H., Koivisto, M., & Revonsuo, A. (2011). Tracking the processes behind conscious perception: A review of event-related potential correlates of visual consciousness. *Consciousness and Cognition*, 972-983.
- Rees, G. (2007). Neural correlates of the contents of visual awareness in humans. *Phil. Trans. R. Soc. B*, *362*, 877-886.
- Revonsuo, A. (2006). *Inner presence: Consciousness as a biological phenomenon*. London: The MIT Press.
- Revonsuo, A. (2009). *Consciousness*. London: Psychology Press.
- Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J. D., & Leventhal, A. G. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology*, *79*, 3272-3278.

- Scholte, S. H., Witteveen, S. C., Spekreijse, H., & Lamme, V. A. (2006). The influence of inattention on the neural correlates of scene segmentation. *Brain Research*, *1076*, 106-115.
- Searle, J. R. (2000). Consciousness. *Annual Review of Neuroscience*, *23*, 557-578.
- Searle, J. R. (2007). Biological naturalism. In M. Velmans, & S. Schneider (Eds.), *The Blackwell Companion to Consciousness* (pp. 325-334). Malden: Blackwell Publishing.
- Shanahan, M. (2010). Localized phenomenology: A recurrent debate. *Cognitive Neuroscience*, *1*(3), 228-229.
- Sligte, I. G., Scholte, H. S., & Lamme, V. A. (2008). Are there multiple visual short-term memory stores? *PLoS ONE*, *3*(2), e1699.
- Supèr, H., Spekreijse, H., & Lamme, V. A. (2001, March). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience*, *4*(3), 304-310.
- Tononi, G. (2004). An information integration theory of consciousness. *BioMed Central Neuroscience*, *4*(42).
- Tononi, G., & Koch, C. (2008). The neural correlates of consciousness: An update. *Ann. N.Y. Acad. Sci.*, *1124*, 239-261.
- Wong-Riley, M. T. (1989). Cytochrome oxidase: An endogenous metabolic marker for neuronal activity. *Trends in Neurosciences*, *12*(3), 94-101.
- Zeki, S. (2003). The disunity of consciousness. *TRENDS in Cognitive Sciences*, *7*(5), 214-218.

Zeki, S., Watson, J., Lueck, C., Friston, K., Kennard, C., & Frackowiak, R. (1991). A direct demonstration of functional specialization in human visual cortex. *The Journal of Neuroscience*, *11*(3), 641-649.