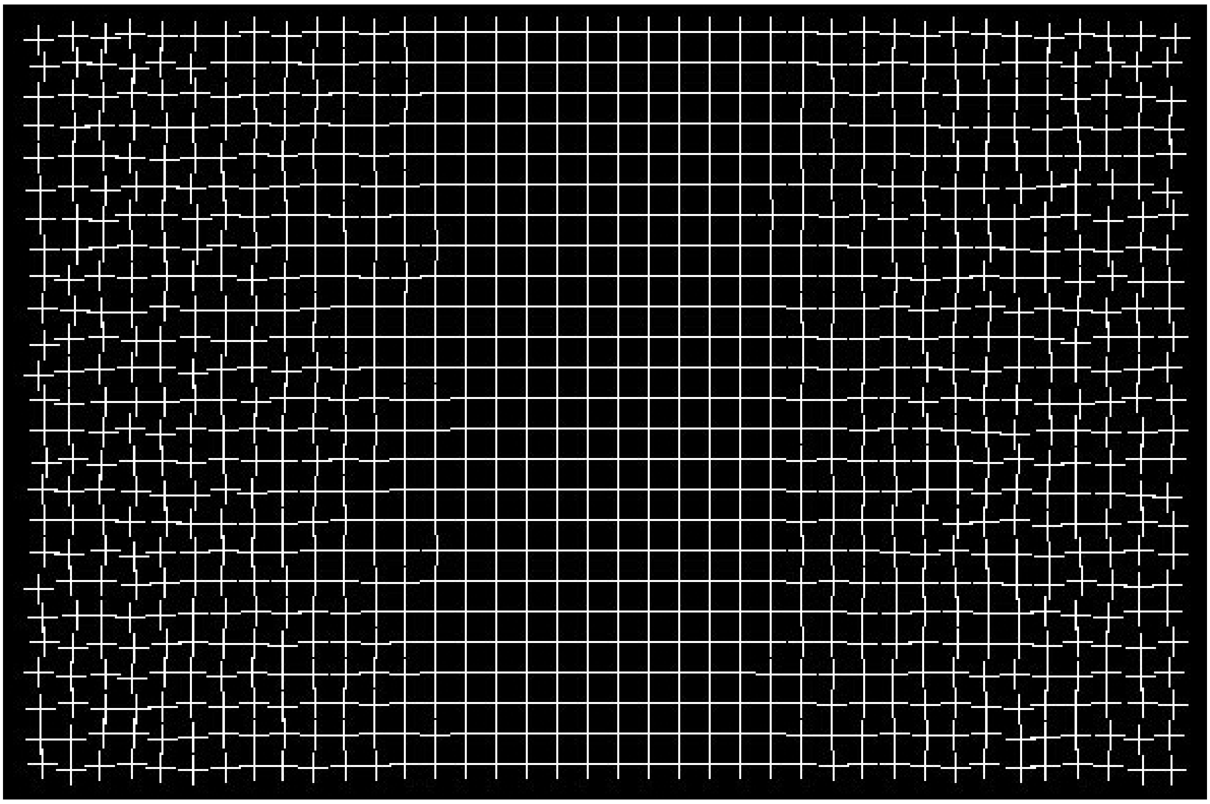
A scientific review on the mechanisms of visual awareness

Student number: s3517799
Author: Jorick te Velde
Date: 27/04/2021
Course: Bachelor's Thesis Life Sciences
Supervisor: Aytaç Karabay



Healing grid by Ryota Kanai. (illusionoftheyear.com/2005/healing-grid/.)

Table of Contents

Abstract

Does awareness of visual stimuli emerge in a graded or dichotomous manner? This has been an ongoing debate within the field of cognitive sciences. In this review, several discrete and gradual models will be assessed to elucidate this problem. The *global neuronal workspace theory* (GNWT; Dehaene et al., 1998) and *episodic simultaneous type/serial token model* (eSTST; Wyble et al., 2009) were found to give similar strong evidence of discrete processing of high-level tasks. Gradual accounts granted substantial evidence of gradual processing, but only for low-level percepts (Bar et al., 2001; Grill-Spector et al., 2000). The *levels of processing hypothesis* (LoP; Windey & Cleeremans, 2015) argues for gradual awareness of low-level processing tasks and discrete awareness of high-level processing tasks, offering a consolidating hypothesis for the nature of visual awareness. Additionally, simulations of a thalamocortical column as well as visual working memory research proposed a neural framework of awareness, arguing that neural oscillations play an imperative role in maintaining percepts in the brain (Dehaene & Changeux, 2005). Particularly gamma-band oscillations were said to represent the ignition of the GNW that is responsible for evoking awareness (Andreas et al., 1999; Totoni & Edelman, 1998). Although linking visual awareness to consciousness remains controversial, new modelling and simulation studies on the LoP hypothesis will provide advances towards solving the "hard" problem of consciousness.

Keywords: awareness, gradual, discrete, processing, oscillations, consciousness

Introduction

Consciousness to this day remains unexplained by scientific fields such as psychology, philosophy, and neuroscience. Many theories have tried to explain consciousness with both reductive and non-reductive theories, though there is still no paradigm for the phenomena we all know to be true; we are conscious (Wiese, 2018). One philosopher posits that this is due to the lack of definition for this problem of consciousness. Chalmers (1995) defines the "easy" problems of consciousness as the phenomena that can be explained by research in cognitive science. Examples of "easy" problems include the integration of information, reportability of mental states, the differences between wakefulness and sleep and the focus of attention. The latter will be a primary focus in this thesis.

These "easy" problems have largely been studied in the past two decades (Monti et al., 2008; Wright & Ward, 2008). Yet, no explanation was found for the "hard" problem of consciousness; the experience of being a conscious organism (Chalmers, 1995). Research in information processing might explain the mechanism of how a certain stimulus gives rise to an emotion, but it can't explain the experience of feeling the emotion. The phenomena of experience remain one of the largest mysteries in the science of the mind. As the current definition of consciousness remains ambiguous, it will be reserved for defining experience in this thesis. The relevant literature also defines this as *phenomenal consciousness* (Kouider et al., 2010).

Awareness refers to being aware of a certain sensory stimulus and it acts as an important part of being conscious. Awareness is often seen as synonymous with consciousness (Block, 2001) so for the sake of clarity, the aforementioned definition will be used in this review. Some philosophers argue that consciousness can not be explained by physical properties, which is often referred to as non-reductive physicalism (NRP; Wilson, 2010). Others posit that by uncovering the physical properties of the brain, the experience of consciousness can be explained. This is often referred to as reductive physicalism (Schneider, 2013). Ultimately, the physical properties of the brain manifest the experience, therefore reductive physicalism is endorsed in this review. Elucidating the mechanisms of awareness, the topic of this thesis, might provide new insights in the nature of consciousness.

Several theories have been posed to explain the mechanisms and nature of awareness and recently it has been a topic of scientific debate (Dux & Marios, 2009; Overgaard et al., 2006). Awareness theories typically fall into two categories; discrete models and gradual models. These conflicting theories follow from electroencephalogram (EEG) and functional magnetic resonance imaging (fMRI) studies as well as behavioural measures (Potter & Levy, 1969). One of the behavioural tasks that has been widely used in awareness research is Rapid Serial Visual Presentation tasks (RSVP). An RSVP involves presenting subjects with a sequence of stimuli at the same spatial location. Discrete models largely focus on the observed attentional blink (AB), which describes the subjects reduced ability to identify a second of two targets (Target 1 = T1, Target 2 = T2) in a stream of distractors, if T2 appears within 200-500 milliseconds of T1 (Broadbent & Broadbent, 1987; Raymond et al., 1992).

Chun & Potter (1995) argued that because of capacity limitations in visual processing resources, T2 is not reported during the AB. This discrete model argues that stimuli are processed in two different stages and because the latter stage fails to process stimuli simultaneously, T2 will be discarded due to occupation of T1. This so-called two-stage model was later refined, but still serves as a basis for most discrete models which will be discussed in more detail. A gradual explanation has been proposed by Elliot et al., (2016) regarding the AB. They tested reportability of different features of T1 and T2 and found that subjects were able to accurately report one feature of both targets like colour, while still showing an AB for the identity of T2. This indicates that awareness of a feature of the object might be possible without awareness of the entire object. Yet another study proposes that awareness is both discrete and gradual (Figure 1), arguing that a low-level stimuli might be partially processed, whereas a high-level stimuli is processed in an all-or-none fashion (Partial Awareness Hypothesis (PAH); Kouider et al., 2010). The models mentioned above are in clear contradiction which has yet to be settled within the scientific community (Asplund et al., 2014; Windey & Cleeremans, 2015). Therefore, this review will attempt to answer the question: Is awareness discrete or gradual? To elucidate this problem, the most compelling models will be assessed and compared. Additionally, computer modelling studies will be discussed to provide a thorough overview. Conclusions on the nature of awareness will then be linked to consciousness in order to tackle the "hard problem".

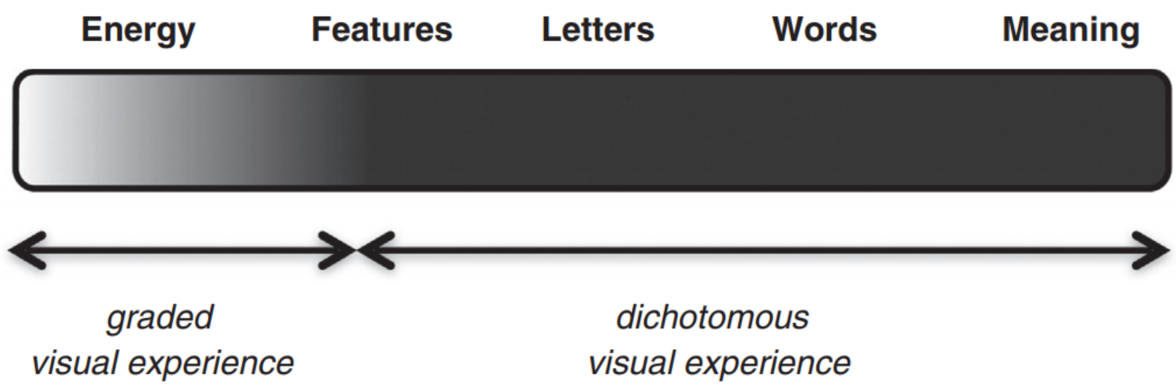


Fig. 1. The spectrum of visual experience proposed by the PAH. Here low-level stimuli are processed in a graded manner, whereas it becomes dichotomous from the featural level onwards (Windey & Cleeremans, 2015).

Models for awareness

Global Neuronal Workspace Theory

Two large advocates for the discrete model of awareness are Sergent & Dehaene (2004). They posed an all-or-none transition of awareness using the attentional blink phenomenon. Targets and distractors presented in the same spatial location and dimensions using RSVP were tested. Subjects were asked to rate T2 visibility on a continuous scale with 21 points which were invisible for the subject. Results showed that subjects only reported at extremes of the rating scale when presented with the AB. This result shows a discrete loss of awareness of T2 when presented with the AB. Sergent & Dehaene link this effect to the two-stage model discussed above (Chun & Potter, 1995), but this model fails to explain the underlying neuronal mechanisms. The global neuronal workspace theory (GNWT; Dehaene et al., 1998; Baars, 1997) was proposed to explain these mechanisms, arguing that the first stage constitutes the automatic processing of a stimulus by a series of brain regions in a bottom-up order. The second stage then gives top-down amplification. Interactions between bottom-up and top-down signalling are said to reinforce each other, activating a network of distinct cortical areas by long-distance excitatory axons. The entry of the stimulus within this global neuronal workspace is then thought to give rise to awareness of the stimuli. However, if the stimulus does not reach the threshold to activate top-down amplification the GNW is not activated and thus the stimulus is not processed.

The GNWT has been criticised for its stance on consciousness. Block (2001) argues that the GNW only explains global accessibility of information, but not for the phenomenality of consciousness that is the experience. Literature is still divided on this position, where some claim that global availability of information is a conscious state by itself (Dennett, 1993). Others claim these are two different phenomena (Block, 2001).

Dissociation between discrete and gradual model methodology

Additional criticism focused on the methodology of the paper. Overgaard et al. (2006) contended that the continuous scale used in the experiments caused subjects to give rating towards the extremes of the scale and therefore, the results favouring a discrete model hypothesis are not subjective and cause biased data. Moreover, Sergent & Dehaene (2004) used a mask following a target stimuli in experiment 2, which caused subjects to give more continuous ratings on the scale. While this result contradicts their conclusion, no explanation was given. A previous study introduced the Perceptual Awareness Scale (PAS), which consists of 4 points, rating from no experience to clear experience (Overgaard et al., 2004). The authors proposed that if subjects scored on the extremes of this scale, it could support dichotomous models. Yet, they found gradual scoring using this dichotomous scale. A study that allowed subjects to create their own rating categories also found more continuous rating behaviour (Ramsøy & Overgaard, 2004). These important differences have subsequently led to differentiation in methodology between discrete and gradual models. This is also reflected in the methodology of the other models which are further discussed below (Bar et al., 2001; Windey et al., 2013).

Modelling of the GNWT

Further studies aimed to simulate the activation of a global neuronal workspace within computer models (for review, see Dehaene & Changeux, 2011). One study modelling a thalamocortical column showed that spontaneous oscillatory behaviour in a single neuron could instigate transient periods of synchronous firing in the column (Dehaene & Changeux, 2005). This sudden emergence of oscillations in membrane potential was observed at a precise threshold of a depolarizing current (-1.1 μA/cm2), producing oscillations starting at 30-35 Hz and increasing slowly towards 40-45 Hz (Figure 2). These oscillations show similar properties to intracellular recordings of thalamic and cortical neurons and are known as gamma-band oscillations (Llinas et al., 1998; Pedroarena & Rodolfo, 1997), which have been argued to explain awareness of sensory stimuli and consciousness (Andreas et al., 1999; Totoni & Edelman, 1998). The paper further proposes that the threshold of the depolarizing current represents the minimal strength a bottom-up stimuli needs to activate top-down self-amplification and gamma-wave oscillations represent the ignition of the global neuronal workspace in the GNW model. In an earlier modelling study they revealed that this ignition suppresses surrounding neurons due to hyperpolarization, creating competition for subsequent stimuli to enter the workspace (Dehaene et al., 2003). This offers a potential neurophysiological explanation for the discrete models of visual awareness.

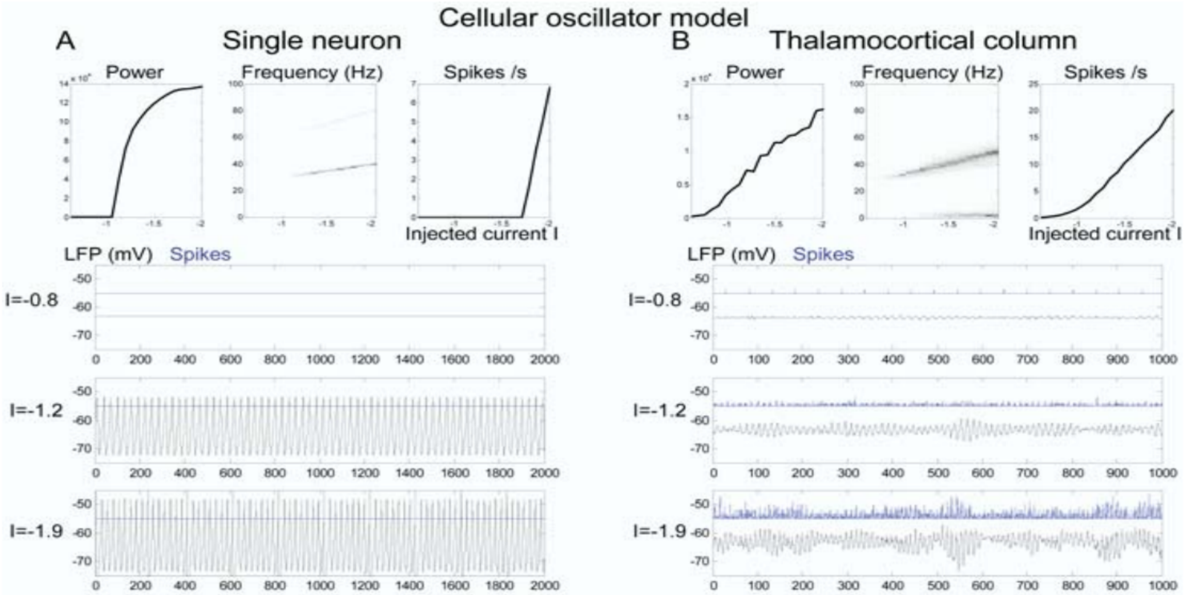


Figure 2. The oscillator model, showing the power of the LFP (top left), frequency (top center) and mean firing rate of pyramidal neurons (top right) based on injected current (I). The graphs below show the spikes (top trace) and the evolution of the LFP over time (bottom trace). The model simulated intrinsic cellular oscillations. There is a notable emergence of oscillations in thalamocortical column graphs at I = 1.2 and 1.9, increasing in strength based on injected current (Dehaene & Changeux, 2011).

Episodic Simultaneous Type/Serial Token Model

Another model has been proposed based on the aforementioned two-stage model (Chun & Potter, 1995) which gives an account for the neural mechanisms of the two stages. The episodic simultaneous type/serial token (eSTST; Wyble et al., 2009) model suggests that the AB is due to the process of separating targets episodically from each other. Stimuli in RSVP are identified because of *type activation* at the conceptual stage. The identity of this information is subsequently bound to a *token* in the working memory to provide episodic information. The binding of the type representation to a token requires attentional enhancement instigated by target detection in the RSVP. This attentional enhancement is regulated by a *blaster,* a single node that receives excitatory signals from target input and inhibitory signals from the *binding pool* which regulates binding of types to tokens. It is the resolution between these competing signals that determines whether the blaster attentionally enhances the target stimuli. The model explains the AB occuring due to suppression of T2 being linked to a token and consolidated into working memory.

The eSTST model was originally developed to account for the phenomena *lag 1 sparing* and *spreading of sparing,* which posed a problem for a previous theory (STST; Bowman & Wyble, 2007). *Lag 1 sparing* refers to the ability of subjects to report T2 if it appears within 50 - 150 ms of a highly salient stimulus, while T2 reportability remains severely impaired when a distractor is shown between targets with the cost of order reversals. S*pearing of the sparing* refers to the ability of subjects to report three or four consecutive targets without a blink, resulting in best reportability for T2 (Nieuwenstein et al., 2005; Olivers et al., 2007). The eSTST model ascribes these phenomena to a temporal window of attentional enhancement prompted by observing T1. Inhibitory and excitatory connections from the working memory control the level of attention, allowing for subsequent targets to excite attention. Inhibition occurs after no new information precedes the last target within 200 ms. This allows the visual system to episodically separate stimuli that are not associated (T1 and T2 separated by a distractor) and episodically link stimuli administered in sequence (spreading of the sparing). The paper notably criticizes accounts focusing on capacity limitation in visual processing, like the two-stage model and the global neuronal workspace model (Chun & Potter, 1995; Sergent & Dehaene, 2004). They argue that because subjects are able to process sequential targets during RSVP, it can not be the limitation of cognitive resources that produces the AB.

A clear distinction should be made regarding these discrete models. The GNW model seems to focus more on the emergence of awareness of stimuli, reasoning that top-down amplification allows stimuli to enter the global neuronal workspace. The eSTST seems to focus on the mechanisms of visual processing rather than awareness, which opens the possibility for combining these two models. The eSTST and GNW model both argue for top-down amplification of the input stimuli, though eSTST refers to this as a *blaster*. Additionally, this top-down amplification is said to determine whether stimuli proceed to higher-level processing in both models. The eSTST further argues that the binding pool sends inhibitory signals to the blaster. This is similar to how ignition of the global neuronal workspace hyperpolarizes surrounding neurons, creating competition for subsequent stimuli to enter the workspace. Differences lie in explanation rather than mechanism, where the eSTST model gives a theoretical account and GNW simulations give a neurophysiological framework. Instead of concentrating on contradictions, combining these models might prove to strengthen a discrete model of awareness.

ERPs during the attentional blink

The discrete models discussed above naturally assume that the target stimulus reaches awareness post-perceptually. Yet, this conjecture has not been discussed by either of the aforementioned theories. Therefore, Vogel et al. (1998) incorporated event-related potentials (ERPs) to examine the continuity of processing between the stimulus and the response in the AB paradigm. ERPs record the synchronous neural activity during specific events. The ERP waveform shows fluctuations, often called components, that indicate the progression of processing during an event.

Results of the study particularly identified no suppression of the P1 and N1 components during the AB. These P1 and N1 components are typically associated with perceptual rather than post-perceptual processing. Furthermore, spatial attention experiments typically show suppression of these components when stimuli are presented at ignored locations (Eimer, 1994; Luck et al., 1994). Additionally, the N400 component showed no suppression during the AB. Previous experiments indicate that the N400 component illustrates the identification of the stimulus (Besson et al., 1992). This result suggests that the AB is induced by a loss of information after stimulus identification. Lastly, the P3 component was fully suppressed during the AB. The P3 component indicates that a stimulus has reached the level of working memory (Donchin & Coles, 1988). In other words, P3 components demonstrate post-perceptual processing as a stimulus has to be identified and categorized before it can enter working memory. These results indicate that T2 is unable to enter working memory, while still preceding perceptual processing reflected by the N400 component.

This conclusion can advocate for both discrete and gradual models of visual awareness. The observed stimulus is processed to some degree favouring gradual models, while it is unable to enter working memory in a discrete way. Though the authors argue that because the N400 component shows no suppression, there is no capacity-limitation at the level of perceptual processing. Rather, the capacity-limit is caused by the visual working memory (VWM), which is reflected by the P3 component. Therefore, the authors argue for a discrete model of awareness. They further contend that stimuli can be identified faster than they can be processed by post perceptual systems and that this strengthens the case of perception without awareness, as stimuli can be identified and perceptually processed but not retained. This points to the critical role that VWM plays in awareness.

Lastly, this study also highlights a downside of RSVP studies that only use reportability as data points. Reportability relies on retention of the stimuli and therefore VWM, as subjects might still be aware of target stimuli while being unable to retain them.

Gradual increases in object recognition

The discrete models have offered detailed accounts for describing the nature of awareness, yet several studies involved in object recognition provide compelling counter-arguments (Overgaard et al., 2006; Elliot et al., 2016; Windey & Cleeremans, 2015; Bar et al., 2001; Grill-Spector et al., 2000). Bar's neuroimaging study particularly focused on identifying recognition-related brain areas (Bar et al., 2001). The experiments administered stimuli to the subjects during MRI scanning. The stimuli used in the trials included line drawings of familiar objects such as tools, clothes and means of transportation. The brain scans showed large differences in recognition of masked and unmasked object pictures. By combining MRI and subject recognition rating, data was collected showing activity at various recognition levels (Figure 3). The scale indicated the degree of recognition, where 1 implied no recognition and 4 implied full recognition of the object. Notably two sites showed a linear increase in activity as a function of recognition success; the occipitotemporal sulcus, an area previously associated with processing shapes (Malach et al., 1995) and the fusiform gyrus. When brain activity was compared between recognition rating 3 ("almost" recognized) and 4 (recognized), specifically the occipitotemporal sulcus and anterior fusiform gyrus showed increased activity with successful object recognition (Figure 3). This indicates that activity in these areas is critical for transferring from almost recognizing an object to becoming fully aware of its identity, especially considering that areas which are known to be involved in low to mid level visual processing, did not show differences in activity in this comparison.

These results indicate gradual increases of activity in visual processing related areas as a function of recognition. Though Bar et al. (2001) conclude that this contradicts discrete changes in cortical activity, the comparison of brain activity (figure 3) indicates discrete differences in cortical activity between partially recognizing an object and being aware of it. Therefore this paper seems to support the aforementioned partial awareness hypothesis (Kouider et al., 2010), with gradual processing until a certain level followed by higher-level dichotomous processing. The fusiform gyrus is of particular interest, as it shows gradual increases in activity with lower levels of recognition with a sudden shift to anterior activity as subjects become aware of the object. The authors further suggest that the anterior fusiform gyrus is responsible for activating semantic knowledge and memory consolidation, while posterior areas focus on pre-recognition analysis. Lastly, it should be emphasized that because these areas are strictly associated with visual awareness, it is unclear whether they are associated with the neural correlates of consciousness. Yet, establishing the precise neural connections that cause a shift from "almost" recognized to full recognition might provide some insight in how visual awareness arises.

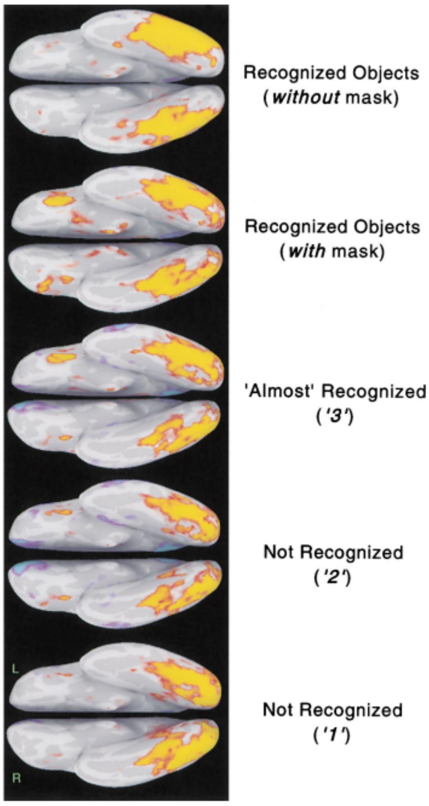


Fig 3. fMRI scans during object recognition experiments. (left) shows average brain activity of subjects during various reported levels of object recognition. (right) shows average difference in brain activity of subjects who reported a rating of 4 and subjects rating a 3 (Bar et al., 2001).

Correlates between recognition performance and the lateral occipital complex. Another study (Grill-spector et al., 2000) also showed evidence for gradual object recognition. Here, two identical masking experiments were set up in which pictures were presented for various durations (500, 120, 40 or 20 ms) immediately followed by a mask. The masks were created by randomly scrambling the images and experiment 1 tested naive subjects, whereas experiment 2 was performed after 5-7 days of training. fMRI during experiments mainly focused on the occipital lobe and extended to the parietal and temporal lobes. Object recognition varied widely, with very high (>90%) recognition for stimuli administered for 500 or 120 ms. Recognition dropped sharply for 40ms stimuli (18 ± 4%). Therefore, further data focused on 40 ms stimuli. It was shown that recognition performance was correlated with particular cortical activity when stimuli duration was alternated, illustrating that both recognition and cortical activity were functions of stimulus duration. Trained individuals also showed significantly higher object recognition for 40ms stimuli (63 ± 3%) for familiar images. Novel stimuli resulted in lower recognition performance (34 ± 3%), though still showing better performance compared to the non-trained group. These results indicate clear correlations between a subject's ability to report objects and cortical activity in the object-related areas, specifically the lateral occipital complex. Most importantly, it was found that V1 activation was less affected by shorter stimuli presentation compared to cortical areas, which showed a drastic difference in cortical signal strength between exposure times of 120 and 40ms. This indicates that a minimal exposure time is needed to trigger higher visual areas needed for recognition (Rolls et al., 1999). As recognition is needed for evoking awareness, this study supports a gradual model for lower level processing and a dichotomous model for higher-level visual processing. The paper therefore stands in line with the partial awareness hypothesis (see introduction).

Levels of processing hypothesis

As a number of studies presented compelling evidence that supports the partial awareness hypothesis (Grill-spector et al., 2000; Bar et al., 2001), it will be further discussed and reviewed. The PAH paper conveys similar criticism of the GNWT as Block (Block, 2001) and argues that the PAH might close the gap between *access consciousness* and *phenomenal consciousness* (Kouider et al., 2010). *Access consciousness* is restricted to the cognitive mechanisms in the brain. It underlies the access to conscious contents, without focussing on how these contents arise. *Phenomenal consciousness* on the other hand explicitly refers to the evoking of consciousness. In addition, the phenomenal experience is believed to be much richer than *access consciousness* can account for (Block, 1995; Block, 2001).

Kouider at al. (2010), argues that the richness of phenomenal consciousness could be explained by the combination of prior information and bottom-up signals, resulting in perceptual illusions. More specifically it proposes that even though the environment contains a large amount of information, only a few features are processed and combined with memory to evoke a rich experience that we call *phenomenal consciousness.* Whether phenomenal consciousness is fundamentally inaccessible, remains unanswered to this day.

A recent variation of the PAH has gained a lot of attention in the field; the levels of processing (LoP) hypothesis (Windey et al., 2013). Similarly, the LoP hypothesis attempts to combine dichotomous and gradual accounts for awareness. For the trials, a simple object recognition task was performed. Subjects were shown a coloured number (red or blue) and asked to report recognition for one of the two features on a perceptual awareness scale rating from one to four. The rating scale was adopted from previous studies criticizing the methodology of the GNWT (Ramsøy & Overgaard, 2004; Overgaard, 2006). Results showed that colour identification resulted in a gradual increase of rating as a function of exposure time, whereas number identification showed a more non-linear increase of rating as a function of exposure time. Because only two colours were used, colour identification was inferred as a low-level processing task, whereas number identification was inferred as a high-level processing task. Indeed the low-level task showed more gradual increases in rating while the high-level task showed more discrete rating. This indicates that insufficient stimulus strength for high-level processes, like number identification, impedes the ability for subjects to report this feature, yet allows them to report low-level percepts like colour. The ability of the subject to become aware of a given stimulus is therefore dependent on stimulus strength and the required level of processing.

A critical review on the LoP hypothesis concludes that although the hypothesis is mostly validated by behavioural as well as brain-based evidence, some of the methodology remains problematic (Jimenez et al., 2020). They contend that the used definition of low-level processing tasks and high-level processing tasks remains ambiguous and that experimental results based on this categorization may lead to precarious results. Therefore, the LoP framework should seek to define these levels of processing more clearly. Furthermore, low-level processing tasks are usually more continuous in nature. For example colour, which is said to require low-level processing, is more continuous in nature. High-level stimuli, like letters, are more discrete in nature. It is therefore possible that the dichotomous and gradual performance results are due to the nature of the task, rather than the level of processing.

Neural correlates of visual working memory and its role in awareness

The connection between working memory and awareness has already been proposed by the aforementioned eSTST model (Wyble et al., 2009; Swan & Wyble, 2014).
In addition, the EPR study revealed that T2, which is not perceived, in an AB experiment goes through perceptual processing, but not working memory. This indicates the importance of the VWM in awareness of the stimuli. A recent review on the system of VWM shines some new light on the nature of VWM, and might offer new perspectives on the nature of awareness (Luck & Vogel, 2013). The review points out the dispute between discrete and gradual models that try to explain VWM. Studies on VWM typically include change detection experiments which differ from RSVP. Change detection relies on memory of spatial location as well as features, like colour or shape (Figure 4).

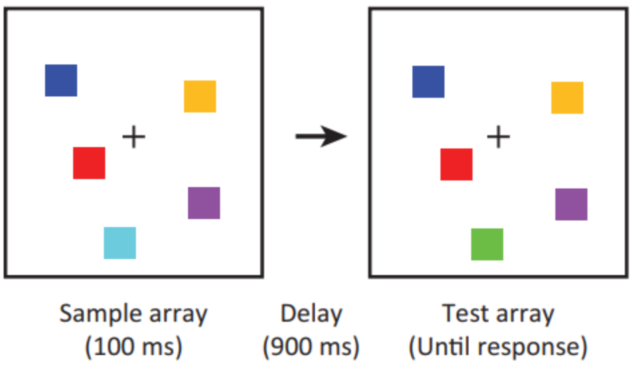


Fig 4. A change detection experiment, where participants are required to remember spatial location and features of target objects (Luck & Vogel, 1997).

In these tasks, subjects are able to maintain three to four objects at a time, varying between individuals (Luck &

Vogel, 1997). Event-related potentials (ERPs) were measured during change detection tasks. By examining ERP recordings during the memory retention interval, in which the stimuli were not presented, activity involved in VWM could be measured. A sustained change in voltage was observed during this delay, an effect called *contralateral delay activity* due to it being found in the hemisphere contralateral to a set of lateralized objects during testing. *Contralateral delay activity* increases with object set size, reaching a peak at the capacity limit of three to four objects (Vogel & Machizawa, 2004).

One theory suggests that the capacity of the VMW is due to a discrete slot-based mechanism. This theory assumes that a maximum number of items can be stored in VWM at a given time. When more items are shown, only a maximum number of items fill the slots and are stored in the VWM with no information processing of subsequent stimuli (Luck, 2008). The resource-based theory suggests that resources are spread among all shown items (van den Berg et al., 2012). The latter theory would propose a gradual reduced precision as set size increases, whereas the slot-based theory predicts a sharp cut-off point. Though both models have been substantiated by experimental evidence (Anderson et al., 2011; Xu & Chun, 2006; Bays & Husain, 2008; van den Berg et al., 2012), neuroimaging data favours slot-based models (Xu & Chun, 2006). ERP and fMRI measures concluded that VWM delay activity increases with set size up till the maximum object capacity, after which activity drops down (Vogel & Machizawa, 2004; Todd & René, 2005). This observation challenges resource-based models as they predict no asymptotic activity, but rather increasing activity, as set size increases.

Current VWM models assume that representations are maintained by feedback loops between different sets of neurons. The maintenance of memories can then be explained by the increased neural activity during the retention period and oscillations of activity bouncing between neural populations (Figure 5a). Singular representations can be maintained by a recurrent feedback loop. Multiple representation upkeep is further explained by several recurrent feedback loops oscillating at different time intervals (Figure 5b). The asynchrony between these oscillations, linked to a given representation, ensures that there is no interference (Deco & Rolls, 2008).

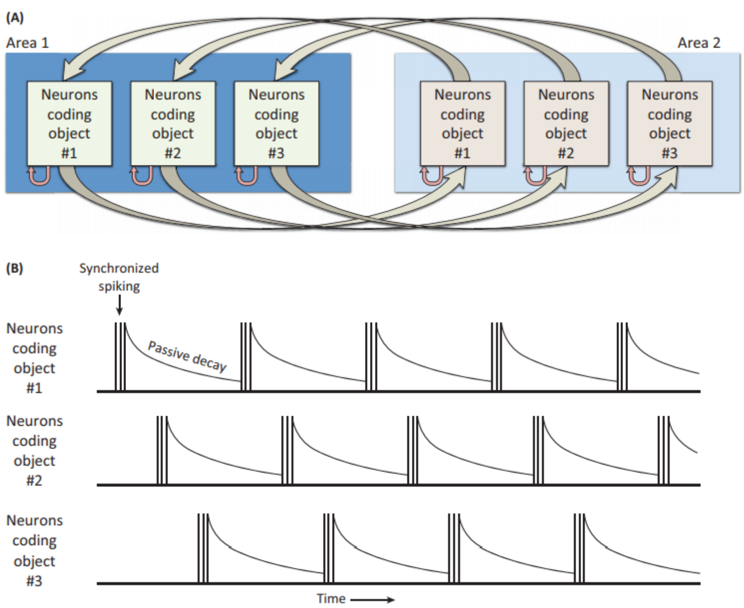


Fig 5. (a) illustrates the recurrent feedback loops between different neural populations.(b) shows the temporal separation of neural oscillations due to stimuli (Luck & Vogel, 2013).

Although the proposed neural mechanism of VWM does not mention GNWT, they have a striking resemblance. Much like the GNWT, figure 5 illustrates that feedback between several brain regions maintains object representation. Awareness constitutes being aware of a certain sensory stimuli and because object representation requires attention to the relevant stimuli, it is practically analogous to awareness. Though GNWT explains awareness of a single stimuli, the model regarding VWM describes maintenance of several stimuli representations. The model can therefore be seen as an extension of the GNWT, which takes into account the temporal aspect of stimuli as well. It should be noted that traditional RSVP studies are focused on the encoding of the stimuli, whereas VWM studies target the maintenance of already encoded stimuli. Nevertheless, combining models that focus on encoding and models that focus on maintenance of stimuli, will provide the most coherent model of visual awareness.

The supposition of the VWM model about activity oscillations (Figure 5b) seems to be supported by GNWT as well (Figure 2b). The previously discussed research about gamma-band oscillations shows significant similarities with activity oscillations between neural populations proposed in the VWM model. Both accounts propose that oscillations play an essential role in object representation in the brain. The only difference being that gamma-band oscillations do not explain multiple object representations at the same time.

Lastly, if stimuli have insufficient temporal separation, synchronised spiking of neurons coding for object one might interfere with neurons coding for object two, resulting in faulty stimuli processing. Therefore, a mechanism that inhibits processing of either stimuli might be favourable for maintaining accurate perception. This mechanism was already proposed by the capacity-limited account of the AB (Sergent & Dehaene, 2004), but can further be substantiated by the neural oscillations seen in the VWM model. On the contrary, this account can not resolve the spreading of the lag 1 sparing and further research would be needed to resolve this issue regarding neural oscillations.

Discussion

By reviewing models of visual awareness and VWM, some persuasive conclusions can be drawn about the nature of awareness. The majority of models that seek to describe the mechanism of awareness attempt to contradict other hypotheses in the field. Yet, several theories have considerable overlap. The GNW model and eSTST model have been shown to chiefly describe the same mechanism in different ways (Dehaene et al., 1998; Wyble et al., 2009). Further simulation studies modelling the GNW found self-sustained oscillations after spiking of singular neurons (for review: Dehaene & Changeux, 2011). This self-sustained quality raises some interesting implications for awareness, as a single stimulus might evoke complex self-sustained oscillations in activity in the brain. This particular research shared a striking resemblance to a proposed mechanism in VWM research (Luck & Vogel, 2013), where neural oscillations explain the retention of objects' spatial location. Therefore, awareness of given stimuli has a strong association with neuronal oscillations, particularly alpha oscillations, within and between brain regions. The primary regions showing specific activation with high-level processing tasks are the lateral occipital complex and the anterior fusiform gyrus (Bar et al., 2001; Grill-spector et al., 2000). Thus, these areas also play an essential role in evoking awareness of stimuli. The discrepancy between activation of brain areas observed in low-level tasks and high-level tasks (Rolls et al., 1999) also indicates that transfer of signals from low to high-level processing areas might be essential for the emergence of awareness.

Due to restraints on the length of this thesis, some compelling gradual models were not covered (Pretorius et al., 2016; Lamme, 2006). Though gradual accounts reviewed above have largely failed to discredit discrete higher-level processing of target stimuli (Bar et al., 2001; Grill-spector et al., 2000). Additionally, discrete models largely focus on higher-level processing tasks (Dehaene et al., 1998; Wyble et al., 2009), meaning that the gradual nature of low-level processing tasks are not refuted (Overgaard et al., 2006; Elliot et al., 2016; Windey & Cleeremans, 2015; Bar et al., 2001; Grill-Spector et al., 2000). The levels of processing hypothesis offers a parsimony following from gradual and discrete models, supporting gradual awareness for low-level processing and discrete awareness for high-level processing (Windey et al., 2013). Combining these gradual and discrete models with the LoP hypothesis provides a feasible account for the nature of awareness. By doing so, we can elucidate how the brain gains access to conscious contents and therefore fully explain *access consciousness.* This could be the focus of a subsequent literature review.

Though compelling, the LoP hypothesis still holds some theoretical problems. First, the hypothesis does not accurately describe the difference between low-level and high-level processing (Jimenez et al., 2020). Therefore, defining a given stimulus as a low or high-level processing task remains precarious. Neuroimaging studies might elucidate this problem by providing detailed accounts on which brain areas are involved in object recognition tasks. Secondly, the nature of the stimulus might determine how it is processed. Features like colour might be gradually processed whereas numbers and letters are discreetly processed. This points to a fundamental problem with the LoP hypothesis; what is the exact threshold between gradual and dichotomous processing? Studies modelling brain areas involved in low and high-level visual processing might provide some key insights in this problem.

The "hard" problem and visual awareness

As these models seek to describe the nature of awareness, the "hard" problem of consciousness remains. The GNWT offers a viable resolution, where single neuron spiking can cause self-sustained neural oscillations. This might explain the emergence of consciousness. Experience might be nothing more than spontaneous oscillatory communication between neural populations instigated by the smallest of sensory stimuli. Though this bears the question whether consciousness exists in the complete absence of sensory stimuli (Block, 2007). This poses a conundrum in cognitive science, as experiments are hard to perform in the complete absence of sensory stimuli and reports. Yet, modelling of neural networks might provide some answers by studying the emergence of neural activity in the absence of stimulation.

Another account of consciousness following the PAH posits that the richness of consciousness is primarily an illusion (Kouider et al., 2010). A study noticed that the weaker the signal, the stronger the subjects would rely on previous information, creating perceptual illusions (Kouider et al., 2007). Additionally, change detection experiments concluded that up to 3 or 4 objects could be tracked at any given time in the VWM. These results indicate that consciousness is based on a limited amount of sensory stimuli at any given time, generating the rest of the experience based on sensory memory.

Based on the discussed literature, this account is indeed the most compelling for explaining *phenomenal consciousness* and therefore the "hard" problem. Evidence based in AB and VWM studies does not seem to contradict this possible resolution (Dehaene et al., 1998; Baars, 1997; Luck & Vogel, 2013). In addition, evidence of self-sustained neural oscillations does indicate that small stimuli can activate large networks of neural populations which can explain the richness of the experience (Dehaene & Changeux, 2011).

Yet, others posit that explanations like these still only describe *access consciousness,* leaving *phenomenal consciousness* untouched (Block, 2007). Whether *phenomenal consciousness* will remain fundamentally inaccessible or becomes elucidated by a comprehensive theory of the mind will be proven in time, in the rapidly maturing field of cognitive sciences.

References

Anderson, D. E., Vogel, E. K., & Awh, E. (2011). Precision in visual working memory reaches a stable plateau when individual item limits are exceeded. The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 31(3), 1128–38. https://doi.org/10.1523/JNEUROSCI.4125-10.2011

Asplund, C. L., Fougnie, D., Zughni, S., Marois, R., & Martin, J. W. (2014). The attentional blink reveals the probabilistic nature of discrete conscious perception. Psychological Science, 25(3), 824–831. https://doi.org/10.1177/0956797613513810

Baars. (1997). In the theatre of consciousness. global workspace theory, a rigorous scientific theory of consciousness. Journal of Consciousness Studies, 4(4), 292–309.

Bar, M., Tootell, R. B. H., Schacter, D. L., Greve, D. N., Fischl, B., Mendola, J. D., ... Dale, A. M. (2001). Cortical mechanisms specific to explicit visual object recognition. Neuron -Cambridge Ma-, 30, 299–299.

Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. Science, 321(5890), 851–854.

Besson, M., Kutas, M., & Petten, C. V. (1992). An event-related potential (erp) analysis of semantic congruity and repetition effects in sentences. *Journal of Cognitive Neuroscience, 4*(2), 132–49. https://doi.org/10.1162/jocn.1992.4.2.132

Block, N. (1995). On a confusion about a function of consciousness. *Behavioral and Brain Sciences, 18*(2), 227–247. https://doi.org/10.1017/S0140525X00038188

Block, N. (2001). Paradox and cross purposes in recent work on consciousness. Cognition, 79(1), 197–219. https://doi.org/10.1016/S0010-0277(00)00129-3

Block, N. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. Behavioral and Brain Sciences, 30(6), 481–498.

Bowman, H., & Wyble, B. (2007). The simultaneous type, serial token model of temporal attention and working memory. Psychological Review, 114(1), 38–70.

Broadbent, D. E., & Broadbent, M. H. P. (1987). From detection to identification: response to multiple targets in rapid serial visual presentation. Perception & Psychophysics, 42(2), 105–113. https://doi.org/10.3758/BF03210498

Chalmers, D.J. (1995). Facing up to the problem of consciousness. Journal of Consciousness Studies, 2(3), 200–219.

Chun, M. M., & Potter, M. C. (1995). A two-stage model for multiple target detection in rapid serial visual presentation. Journal of Experimental Psychology. Human Perception and Performance, 21(1), 109–27.

Deco, G. and Rolls, E.T. (2008) Neural mechanisms of visual memory: a neurocomputational perspective. In Visual Memory (Luck, S.J. and Hollingworth, A., eds), pp. 247-289, Oxford University Press

Dehaene, S., & Changeux, J. P. (2011). Experimental and theoretical approaches to conscious processing. Neuron, 70(2), 200–27. https://doi.org/10.1016/j.neuron.2011.03.018

Dehaene, S., Kerszberg, M., & Changeux, J.-P. (1998). A neuronal model of a global workspace in effortful cognitive tasks. Proceedings of the National Academy of Sciences of the United States of America, 95(24), 14529–14534

Dehaene, S., Sergent, C., & Changeux, J.-P. (2003). A neuronal network model linking subjective reports and objective physiological data during conscious perception. Proceedings of the National Academy of Sciences of the United States of America, 100(14), 8520–8525.

Dennett, D. C. (1993). Consciousness explained. Penguin uk.

Donchin, E., & Coles, M. G. H. (1988). Is the p300 component a manifestation of context updating? *Behavioral and Brain Sciences, 11*(03), 357–357. https://doi.org/10.1017/S0140525X00058027

Dux, P. E., & Marois, R. (2009). The attentional blink: a review of data and theory. Attention, Perception & Psychophysics, 71(8), 1683–700. https://doi.org/10.3758/APP.71.8.1683

Eimer, M. (1994). “sensory gating” as a mechanism for visuospatial orienting: electrophysiological evidence from trial-by-trial cuing experiments. *Perception & Psychophysics*, *55*(6), 667–675. https://doi.org/10.3758/BF03211681

Elliott, J. C., Baird, B., & Giesbrecht, B. (2016). Consciousness isn't all-or-none: evidence for partial awareness during the attentional blink. Consciousness and Cognition, 40,79–85. https://doi.org/10.1016/j.concog.2015.12.003

Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object-selective activation correlates with recognition performance in humans. Nature Neuroscience, 3(8), 837–43.

Jimenez, M., Hinojosa, J. A., & Montoro, P. R. (2020). Visual awareness and the levels of processing hypothesis: a critical review. Consciousness and Cognition, 85.

Kouider, S., Dehaene, S., Jobert, A., & Le Bihan, D. (2007). Cerebral bases of subliminal and supraliminal priming during reading. Cerebral Cortex, 17(9), 2019–2029.

Kouider, S., de, G. V., Sackur, J., & Dupoux, E. (2010). How rich is consciousness? the partial awareness hypothesis. Trends in Cognitive Sciences, 14(7), 301–7. https://doi.org/10.1016/j.tics.2010.04.006

Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. Trends in Cognitive Sciences, 10, 494–501.

Llinas, R., Ribary, U., Contreras, D., & Pedroarena, C. (1998). The neuronal basis for consciousness. Philosophical Transactions: Biological Sciences, 353(1377), 1841–1849.

Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994). Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology. Human Perception and Performance, 20*(4), 887–904.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. Nature, 390(6657), 279–81.

Luck, S. J. (2008). Visual short-term memory. In Visual memory, pp. 43-85, Oxford University Press

Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: from psychophysics and neurobiology to individual differences. Trends in Cognitive Sciences, 17(8), 391–400. https://doi.org/10.1016/j.tics.2013.06.006

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., ... Tootell, R. B. H. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proceedings of the National Academy of Sciences of the United States of America, 92(18), 8135–8139.

Monti, J. M., Pandi-Perumal, S. R., & Sinton, C. W. (2008). Neurochemistry of sleep and wakefulness. Cambridge University Press. INSERT-MISSING-URL.

Nieuwenstein, M. R., Chun, M. M., van der Lubbe, R. H. J., & Hooge, I. T. C. (2005). Delayed attentional engagement in the attentional blink. Journal of Experimental Psychology : Human Perception and Performance, 31(6), 1463–1475.

Olivers, C. N. L., van der Stigchel, S., & Hulleman, J. (2007). Spreading the sparing: against a limited-capacity account of the attentional blink. Psychological Research : An International Journal of Perception, Attention, Memory, and Action, 71(2), 126–139. https://doi.org/10.1007/s00426-005-0029-z

Overgaard, M., Feldbæk Nielsen, J., & Fuglsang-Frederiksen, A. (2004). A tms study of the ventral projections from v1 with implications for the finding of neural correlates of consciousness. *Brain and Cognition*, *54*(1),58–64. https://doi.org/10.1016/S0278-2626(03)00260-4

Overgaard, M., Rote, J., Mouridsen, K., & Ramsøy Thomas Zoëga. (2006). Is conscious perception gradual or dichotomous? a comparison of report methodologies during a visual task. Consciousness and Cognition, 15(4), 700–708. https://doi.org/10.1016/j.concog.2006.04.002

Potter, M. C., & Levy, E. I. (1969). Recognition memory for a rapid sequence of pictures. Journal of experimental psychology, 81(1), 10.

Pretorius, H., Tredoux, C., & Malcolm-Smith, S. (2016). Subjective awareness scale length influences the prevalence, not the presence, of graded conscious states. Consciousness and Cognition, 45, 47–59. https://doi.org/10.1016/j.concog.2016.08.007

Pedroarena, C., & Llinás Rodolfo. (1997). Dendritic calcium conductances generate high-frequency oscillation in thalamocortical neurons. Proceedings of the National Academy of Sciences of the United States of America, 94(2), 724–728.

Ramsøy Thomas Zoëga, & Overgaard, M. (2004). Introspection and subliminal perception. Phenomenology and the Cognitive Sciences, 3(1), 1–23. https://doi.org/10.1023/B:PHEN.0000041900.30172.e8

Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an rsvp task: an attentional blink? Journal of Experimental Psychology. Human Perception and Performance, 18(3), 849–60.

Rolls, E. T., Tovée MJ, & Panzeri, S. (1999). The neurophysiology of backward visual masking: information analysis. Journal of Cognitive Neuroscience, 11(3), 300–11.

Schneider, S. (2013). Non-reductive physicalism and the mind problem. Noûs, 47(1), 135–153.

Sergent, C., & Dehaene, S. (2004). Is consciousness a gradual phenomenon? evidence for an all-or-none bifurcation during the attentional blink. Psychological Science, 15(11), 720–728.

Swan, G., & Wyble, B. (2014). The binding pool model of vwm: a model for storing individuated objects in a shared resource pool. Journal of Vision, 14(10), 160–160. https://doi.org/10.1167/14.10.160

Todd, J. J., & Marois René. (2005). Posterior parietal cortex activity predicts individual differences in visual short-term memory capacity. Cognitive, Affective, & Behavioral Neuroscience, 5(2), 144–155. https://doi.org/10.3758/CABN.5.2.144

van den Berg, R., Shin, H., Chou, W.-C., George, R., & Ma, W. J. (2012). Variability in encoding precision accounts for visual short-term memory limitations. Proceedings of the National Academy of Sciences of the United States of America, 109(22), 8780–8785.

Vogel, E. K., Luck, S. J., & Shapiro, K. L. (1998). Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *Journal of Experimental Psychology. Human Perception and Performance*, *24*(6), 1656–74.

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. Nature, 428(6984), 748–51.

Wiese, W. (2018). Toward a mature science of consciousness. Frontiers in Psychology, 9, 693–693. https://doi.org/10.3389/fpsyg.2018.00693

Wilson, J. (2010). Non-reductive physicalism and degrees of freedom. The British Journal for the Philosophy of Science, 61(2), 279–311. https://doi.org/10.1093/bjps/axp040

Windey, B., & Cleeremans, A. (2015). Consciousness as a graded and an all-or-none phenomenon: a conceptual analysis. Consciousness and Cognition, 35, 185–91.

https://doi.org/10.1016/j.concog.2015.03.002.

Wright, R. D., & Ward, L. M. (2008). Orienting of attention. Oxford University Press.

Wyble, B., Bowman, H., & Nieuwenstein, M. (2009). The attentional blink provides episodic distinctiveness: sparing at a cost. Journal of Experimental Psychology. Human Perception and Performance, 35(3), 787–807. https://doi.org/10.1037/a0013902

Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. Nature, 440(7080), 91–5.