The Crack of Dawn

Perceptual Functions and Neural Mechanisms that Mark the Transition from Unconscious Processing to Conscious Vision

Victor Lamme

There is conscious vision, and there is unconscious visual processing. So far so good. But where lies the boundary between the two? What are the visual functions that shape the transition from "processing in the dark" to having a conscious visual percept? And what are the neural mechanisms that carry that transition? I review the findings on feature detection, object categorization, interference, inference, Gestalt grouping, and perceptual organization, and examine to what extent these functions correlate with the presence or absence of conscious vision. It turns out that a surprisingly large set of visual functions is executed unconsciously, indicating that unconscious vision is much "smarter" than we might intuitively think. Only when these unconscious mechanisms fail, and more elaborate and incremental processing steps are required, is consciousness necessary. The function of conscious vision may be to add a final layer to our interpretation of the world, to solve relatively "new" visual problems, and to enable visual learning.

Keywords
Access | Anaesthesia | Attention | Consciousness | Continuous flash suppression | Feature detection | GABA | Gestalt laws | Human | Masking | Monkey | NMDA | Object categorization | P-consciousness | Perceptual inference | Perceptual interference | Perceptual organization | Phenomenal experience | Qualia | Report | Rivalry | The hard problem | Visual cortex | Visual perception

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1 Qualia 2.0

What do we need to know about consciousness? Which aspect of it is most mysterious? What do we want philosophy, psychology, neuroscience, computer science, or even physics to tell us about consciousness that we do not already know? The answer to that question may vary from person to person. To me it is this very simple thing: why do I see? Why do I have conscious experiences whenever I open my eyes? What makes the 1.5 kilograms of protein and fat in my head give me the wonderful sensations I experience every day, from the second I wake up until the moment I fall asleep?

The point is probably best illustrated by the difference between a digital photo camera and the human mind. A camera nowadays can do wonderful things. It can record an image at extreme resolutions, with the right focus and exposure, all by itself. It can identify a face, putting it in a frame on the screen, and writing the name below it of the person it recognizes. You can leave it to push the button at the moment everybody smiles. Connect it to a com-

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puter, and it will detect emotions, recognize objects, or read handwriting on a letter. Surveillance cameras can detect suspicious movements or strange behaviours in crowds, outperforming human night-guards or intelligence agents. There is one big difference between the camera and the human mind, though. The camera does not see.[1] I do. And so does the night guard, most of the time. It is this aspect of visual processing that is in need of an explanation. Not the fact that I recognize the person in front of me, can read his emotions, talk to him, or pick up the cup of coffee he gives me. I can vaguely understand how my brain enables me to do that. What I do not understand is how it is that I see all those things.

Is that the "hard problem" all over? Am I talking Qualia? Not in the strict sense. In its original formulation, the hard problem would argue that there is no function, no neural process whatsoever that could ever explain conscious sensations (Chalmers 1995). Functions explain functions, but not the fact that I see. Qualia are defined as ineffable aspects of information: the redness of red, stripped of every possible functional property or reactive disposition. And with that comes the whole charade of inverted spectra, colour scientists called Mary, and explanatory gaps. Which didn't get us all that far—so let's not chase that unicorn again.

It's not that I don't want to address the hard problem, or bridge the explanatory gap. That is in fact exactly what I am after (Lamme 2010a, 2010b). But I would like to leave that for later. What we need to recognize, first, is that there must be some functions and some neural processes that are more closely connected to seeing than others (Crick & Koch 1998, 2003). For example, it is fairly reasonable to assume that an understanding of the neural basis of a reflexive motor response—like the pulling away of your hand when it touches fire— does very little towards explaining consciousness (Lamme & Roelfsema 2000; Lamme 2006). Other functions may offer a better gateway. For example because they explain some fundamental aspect of seeing (Seth 2010), such as its unity, or because they coincide with the difference between conscious visual processing and visual processing that occurs "in the dark" (Lamme 2010a, 2010b). In trying to bridge the explanatory gap, I think it is important to first find the right tree up which to bark. We must first identify the exact boundaries between conscious and unconscious processing. The hard problem can then be attacked afterwards. Or maybe that whole explanatory gap will vanish right before our eyes once we are there.

This paper is about exactly that. Let's find the visual functions and neural processes that take us as close as possible to the hard problem, as close as possible towards explaining why we humans see, while photo cameras do not. And let's avoid barking up the wrong tree.

2 Why dolphins are not fish

To find the cognitive functions and neural processes that take us towards understanding the phenomenality of consciousness it is important to establish a boundary—a boundary with what we should call unconscious processing. This will by no means be an easy job (Lamme 2006). In fact, the whole issue of understanding consciousness and solving the explanatory gap is about positioning that boundary. There are situations where it is in fact unclear whether we should talk about a conscious sensation or not. Take the situation of a split-brain patient: here, a stimulus presented to the left visual field will be processed by the right half brain, typically devoid of communication via language. Hence, the subject will *tell* you that she did not see that stimulus. He may draw the stimulus, however, using his left hand. Or the left hand may point at the stimulus, or match it to a related subject (Gazzaniga 2005). Who are we to believe, then? The hand or the mouth? What types of behaviour may count as evidence for conscious sensations? Just speech? What about aphasic subjects, then? Similarly, there are conditions like neglect, or manipulations of attention (change blindness, inattentional blindness),

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[1] Or at least we assume it does not. This is the basic intuition we start from in trying to explain consciousness. If not, one easily slides into pan-psychism. That is a viable option of course: it could be that the camera does see, yet cannot "tell" us. However, the arguments put forward in the remainder of this paper seem to suggest that the camera does not see.

where it is difficult to be entirely sure that what appears to be not seen is in fact maybe just not attended to, and hence forgotten or not cognitively accessible and hence not reportable (Lamme 2003, 2006, 2010). This uncertainty has sparked a lively debate on the nature of consciousness, its potential independence of cognitive functions like attention, working memory, or access (Lamme 2004, 2010a, 2010b), and whether consciousness can ever be separated from a *report* about consciousness (Block 2005, 2007; Dehaene et al. 2006; Cohen & Dennett 2011; Fahrenfort & Lamme 2012). This debate is all about the difference between seeing and knowing, between phenomenality and access (P-consciousness and A-consciousness), between qualia and higher-order thoughts. In this debate, the issue that seems unsolvable is where exactly the boundary between conscious and unconscious processing should be laid.

In such attempts to establish boundaries, it is perhaps good to start from the extremes, as an example from zoology will illustrate. Superficially, one could argue about whether a dolphin is a fish or a mammal. Science has resolved that argument by looking at animals that we all agree are either mammals (such as dogs, cows, or monkeys) or fish (such as sole, tuna, or piranha). From that perspective, the key differences between these species lies in the way they breathe and reproduce.[2] Why are these the key differences? Well, differences in breathing do all the explaining for why fish are generally more adept at living in water instead of on land. Similarly, evolution towards the land has called for eggs with protective layers (amnios), as anamniotic eggs (that fish lay) cannot survive on land. The most extreme version of that is the intrauterine development of the egg. Mammals and fish are thus at the two extreme ends of evolutionary adaptation towards breathing and reproducing on land.[3] We understand why a mammal behaves differently to a fish from these key properties. From these key properties we understand why mammals roam the surface of the earth, why they look the way they look, and why they behave the way they do.[4] In classifying animals, we use these features for a discrete taxonomy. This means that there are other features that do not qualify as defining characteristics, which are disregarded in animal taxonomy. Among these are behaviours like swimming in water, or living in groups. The key differences, obtained from looking at the extreme ends of the spectra, lead us to conclude that dolphins are mammals and not fish, even though appearances may suggest otherwise. We can draw a sharp boundary, and do not have to resort to saying that dolphins are "fishy mammals", because we recognize that the swimming behaviour of dolphins is irrelevant to their taxonomy.[5] *Defining features* and *irrelevant features* enables a proper and discrete taxonomy, making most sense of all the available data. Moreover, a taxonomy based on such features allows for an understanding that goes towards a deeper level, in this case the evolutionary pressure that came from the transition from sea to land dwelling.

I propose to undertake something similar with consciousness. What is the proper taxonomy of conscious versus unconscious vision? What are the defining features of this difference, and what features are irrelevant? And do the defining features take us towards a somewhat more fundamental level of understanding consciousness (Lamme 2010a, 2010b)? To find those features, we start from the extreme ends: the mammals and fish of consciousness research, the things most people will agree on as representing either conscious or unconscious processing.

3 The mammals and fish of consciousness

When I am awake and say I see a face, am able to report its identity; I can identify the colour of its eyes and hair, and judge its emotional ex-

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[2] Among other things, like whether they maintain body temperature or have hairy skin.

[3] With reptiles and birds in between, laying amniotic eggs on the land.

[4] Of course there is the occasional mammal that lays eggs (e.g., the platypus) or fish that give birth to live young (e.g., the hammerhead shark). Still, calling these mammals or fish depends on the relative weight of other defining features, such as their way of breathing, feeding, body temperature maintenance, etc.

[5] In a somewhat more mathematical analogy one could take all properties of all animals in the world, and perform a cluster or factor analysis. A good taxonomy has clusters that are aligned along the primary factors. Traditional taxonomy seems to have operated in this way implicitly.

pression. There is little reason to doubt that I have a conscious sensation of that face.[6] If we study the properties of visual processing in this condition, we can be pretty sure we are studying the properties of conscious visual perception. This is our "mammal" of consciousness. We can study the properties of this species fairly easily. We can resort to introspection, verbal reports, or more strictly formalized approaches like detection or discrimination tasks. In favour of using introspection is that our introspective idea of consciousness is the very thing we are trying to explain. I would like to understand why the world looks the way it looks in my mind's eye. This is the explanandum. Even so, we should be cautious in fully "trusting" introspection,[7] and that is where more formal approaches may come in handy.

What would be the proper "fish" of consciousness? Are there conditions where everyone agrees that consciousness is absent? Dreamless sleep (Tononi & Massimini 2008) and anaesthesia (Alkire et al. 2008) seem to be good candidates, although not very useful ones, given that visual stimuli are difficult to deliver, and that one can only resort to objective measures (brain signals) to assess what is still processed or not. Awake subjects are easier to assess in that respect, but there it is hard to find truly unequivocal manipulations of consciousness. "Unequivocal" in this context means that the manipulation can truly be regarded as a manipulation of consciousness, i.e., in the case of vision is a manipulation of visibility (Kim & Blake 2005; Lamme 2006). An example of the latter would be visual masking (Breitmeyer & Ogmen 2000; Enns & Di Lollo 2000). Here, a target stimulus is presented very briefly, and immediately followed by another stimulus, known as the mask. When properly done, this will render the target completely invisible. People will be at chance detecting presence or absence, or in judging another property of the target stimulus. It is safe to assume invisibility in masking, because there is no conceivable reason that could prevent the subject from reporting his visual percept, had he had one: the subject is sitting there, focussing his full attention to the target location, ready to push the button as soon as he sees the target. The not-seeing can therefore not be attributed to the absence of attention, to a lapse of memory, or to any other cognitive function sitting between a potentially conscious sensation and its report (Lamme 2003, 2010a, 2010b). As we are ready to believe the presence of consciousness in the case of someone verbally describing the face he sees, we should be equally ready to believe its absence in the case of masking (or dreamless sleep and anaesthesia).[8]

Another popular paradigm to render stimuli invisible is continuous flash suppression (CFS; Tsuchiya & Koch 2005. Here, the target stimulus is shown to one eye, while the other eye receives a rapid stream of brightly coloured patches, serving as a mask. This typically results in the target stimulus being rendered invisible, although stimuli may "break through" after a while.[9] A third paradigm is dichoptic masking, where two oppositely coloured stimuli are shown to the two eyes, that when properly fused combine into an invisible stimulus (Mout-

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[6] One could do so, of course, which would lead to the denouncement of consciousness as a scientific phenomenon altogether, much along the lines of eliminative materialism (e.g., Churchland 1981). Daniel Dennett, in his categorical denouncement of anything coming close to qualia or even the phenomenology of consciousness, seems to follow a similar agenda (1993). It is entirely possible indeed that consciousness is a figment of our imagination, one that will evaporate upon close scientific scrutiny. Something like that happened to 'elan vital'—the unique property of living matter—once we learned about chemistry, biology, DNA, and natural selection. For now, let's assume that consciousness exists, and is in need of an explanation. If not, I would rather not be spending my years in neuroscience.

[7] One important caveat is that for introspection we have to resort to cognitive functions like attention, memory, and "internal report". This may result in both a potential underestimation of what we actually see (see for example the iconic/fragile/working memory discussion), and to an overestimation of what we actually see (as in the illusion of peripheral colour vision). This has been dealt with extensively elsewhere (Lamme 2010a).

[8] Note that a proper treatment of response bias is important in this case. "Shy" subjects may feel inclined to respond "not seen" on most trials, more liberal subjects may feel inclined to respond "seen" on most trials. Only treating the responses in terms of signal detection theory (Swets et al. 1978) can truly establish the absence of any sensation (because the number of false alarms—subjects saying "seen" on trials without a target—is taken into account). From that perspective, using only partially-effective masks is not a proper method, not even when only those trials are used in which subjects reported not seeing the target.

[9] A potential problem with the CFS manipulation is that "time to breakthrough" is often used as a measure of relative awareness of stimuli. Time to breakthrough is more or less analogous to a "yes" response (or hit) in a masking paradigm, and hence can suffer from response bias. CFS studies where responses are more rigorously treated in terms of signal detection theory are scarce. See Stein et al. (2011) for a more elaborate discussion on this problem with the CFS paradigm.

oussis & Zeki 2002; Fahrenfort et al. 2012). From all the available neuropsychological patients, patients suffering from hemianopia due to a V1 lesion (often accompanied by blindsight) are probably the clearest cases of impaired visual consciousness (Weiskrantz 1996).

I select these consciousness manipulations because they seem to be the safest bets for highlighting situations where conscious vision is really absent. The absence of conscious vision in these cases has purely visual origins. There is no other function precluding the report of a potentially present visual sensation, as may be the case in split-brain patients or neglect, or in manipulations like innattentional blindness, change blindness, or the attentional blink (Lamme 2003). The two extreme ends—the mammals and fish of consciousness—may serve as a guideline towards establishing the properties of conscious versus unconscious processing. What are the differences between awake conscious vision and vision in sleep, anaesthesia, blindsight, and the various forms of masking?

4 Categorization: From low to high level features

Above, I used the example of seeing a face. What does seeing a face mean, in terms of the visual functions being executed? Recognizing a face first of all entails that one identifies the stimulus as belonging to the class "faces", as opposed to any other class of stimuli, such as "animals", "teapots", "houses", or "letters". This is a process of categorization. Intuitively, categorization seems a key property of consciously seeing and recognizing a face. It is not, however. Since the first findings of blindsight it has been recognized that categorization can occur fully independently of conscious sensations (Weiskrantz 1996; Boyer et al. 2005). Patients without awareness of stimuli in the blind part of the visual field can nevertheless categorize these stimuli, as long as the categorization is framed in a two-alternative forced choice: is it a square or a circle, is it moving upwards or downwards, is it red or green, vertical or horizontal? In such cases, patients' responses fall well above mere chance, indicating that the categorization of stimuli in two distinct classes is still functioning, and hence does not necessarily require consciousness.[10]

Categorization is the main function of cortical visual neurons, in that each neuron is *feature-selective*: it only responds to a stimulus when that stimulus possesses certain visual features. A Nobel prize was awarded for this finding, as it is fundamental to the operation of the visual cortex (Hubel 1982). It ranges from low level features such as spatial frequency, orientation, direction of motion, or colour to higher-level features such as the geometry of a shape or the class of an object. Each feature-selective neuron can be seen as doing a simple, often one-dimensional categorization: it signals "vertical orientation", "moving upwards", or "rectangular shape" (Lamme & Roelfsema 2000). Face-selective neurons shout "face!" (Oram & Perrett 1992). The categorization responses of visual neurons are so fundamental to their operation that they are fully independent of consciousness: most neurons are equally feature selective in anaesthesia as they are in the awake condition (Dow et al. 1981; Snodderly & Gur 1995; Lamme et al. 1998a). Feature-selective responses of neurons are mediated via feedforward connections, and visual categorization proceeds along these feedforward connections in an unconscious way (Lamme et al. 1998b; Lamme & Roelfsema 2000).

Additional evidence dissociating categorization from consciousness comes from a multitude of sources. Unseen stimuli in backward-masking are also categorized, as can be judged from the specific priming effects they may evoke. For example, a fully masked digit 7 may speed up (or slow down) responses to categorizing a second digit (or number word) as either being above or below 5, showing that the masked and unseen number (the 7) is categorized according to its numeric value (Dehaene et al. 1998).[11] Many similar examples exist. Moreover, it has been shown that masked and hence unseen stimuli evoke category-specific responses from the brain, either in the form of se-

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[10] Note, however, that categorization is typically far better for stimuli than patients—or normal subjects—are aware of.

[11] Or more precisely: as being either below or above 5, in this experiment.

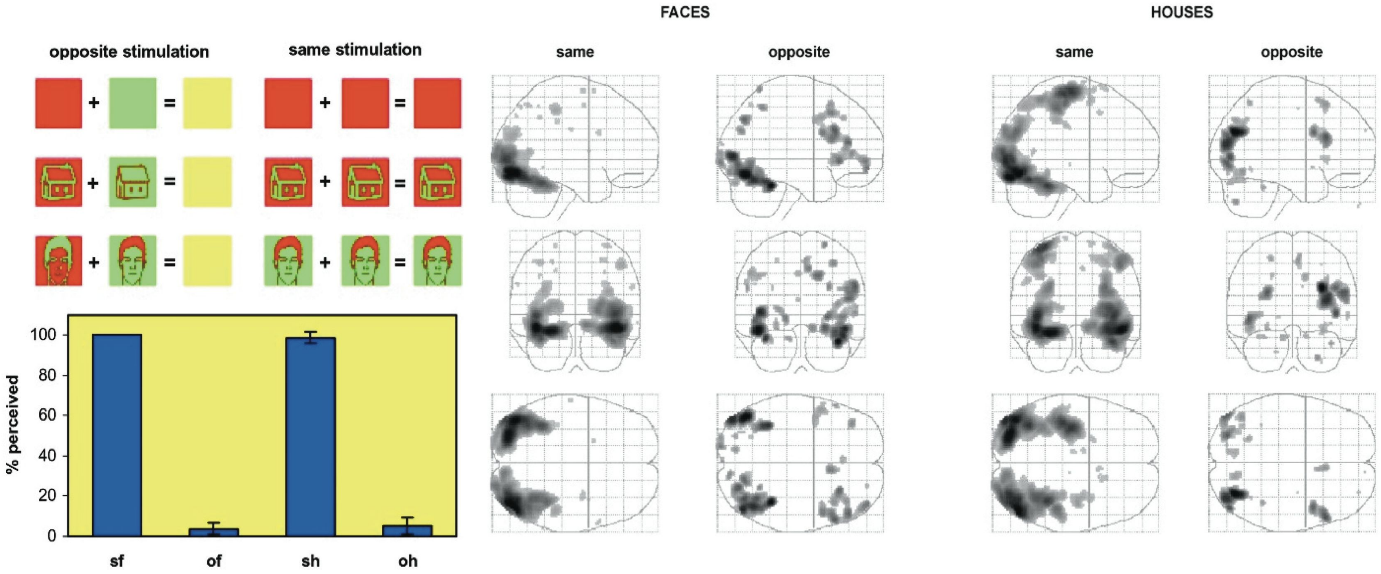

Figure 1: Faces and houses were made invisible using dichoptic masking—i.e., presenting oppositely coloured versions to each eye. Regardless of (in-)visibility, these faces and houses evoked selective activations of category specific regions of the brain (from: Moutoussis & Zeki 2002).

lective single unit responses (Rolls & Tovee 1994; Macknik & Livingstone 1998), or in the form of selective activation or category-selective regions such as the Fusiform Face Area (FFA) (figure 1) (Moutoussis & Zeki 2002; Kouider et al. 2009),[12] or in the Visual Word Form Area (Dehaene & Naccache 2001)—indicating that they are categorized up to the level of face vs non-face or word vs non-word (Dehaene et al. 2004). There is a large body of literature covering the unconscious processing of emotional valence in either faces or words (Straube et al. 2011).

Particularly far-reaching levels of unconscious categorization have been reported for behaviourally or socially relevant stimuli. Tools evoke selective activation of the dorsal stream areas—and selective priming effects—when made invisible with CFS (Fang & He 2005; Almeida et al. 2008). Faces that have their eyes turned towards the viewer break from CFS sooner than faces that are turned away—a finding that is probably explained by the fact that faces turned towards the viewer pose a very relevant or even threatening social signal (Gobbini et al. 2013). Similarly, the gender of naked bodies is processed during CFS (Jiang et al. 2006). Also, the mismatch between object categories is identified for stimuli made invisible using CFS: scenes with mismatching objects (e.g., a cook taking a chess-board out of the oven instead of a dish) break from CFS sooner than matching scenes (Mudrik et al. 2011).

The latter finding is related to various non-visual "categorization" processes that occur for invisible stimuli: it has been shown that masked stimuli travel throughout the brain, even reaching high-level areas involved in inhibitory cognitive control, response error selection, or evidence accumulation, exerting high-level cognitive effects (Van Gaal & Lamme 2012). So invisible stimuli not only activate visual categorization processes, but also activate extremely high-level and very abstract categories such as the stimulus being a "stop signal", an "error", or "evidence for a right button press".

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[12] It is unclear to what level invisible faces are processed exactly. Clearly, face/non-face categorization takes place for masked stimuli (see below), but whether face identity is also preserved depends on the exact experiment. Some find face-*identity*-specific priming and suppression of activation of the FFA and related face-selective-regions for backward masked stimuli (Kouider et al. 2009). However, this effect was only present for famous faces, not for unknown faces, showing that it may not be identity itself that is processed but "level of fame" or something similar. Others have made faces invisible using CFS, and found that face-specific adaptation only occurred for visible, and not for invisible faces (Moradi et al. 2005). The two studies are hard to compare, partly because of the different techniques used to make faces invisible (masking vs. CFS), but mostly because the latter used an adaptation effect as independent variable. It may be that unconscious categorization still occurred, yet did not result in learning (e.g., Meuwese et al. 2013; Meuwese et al. 2014).

From a neural perspective, categorization is feature selectivity, which may range from very simple to highly complex features and categories. This kind of categorization proceeds entirely independent of consciousness.[13] So how does conscious recognition differ from categorization? To answer this question, we have to take a closer look at categorization responses. What a face-selective cells does, is to categorize a face as belonging to the class of faces versus non-faces. That's all. When we consciously see a face, however, we do much more than this: we classify the stimulus as a face, but at the same we identify its shape, colour, identity, and emotional expression. So we distinguish between "that brown face of my sad-looking friend Peter" and very many other faces—and also between that face and millions of other potential visual stimuli.

Gulio Tononi uses the metaphor of a photo-diode to illustrate the point (2008, 2012). For a photo-diode a black screen is different from a white screen. That's a distinction it can make. The photo-diode carries information about the brightness of the screen, so its signal carries one bit of information (or a few bits, depending on its sensitivity). For us, however, consciously seeing a black screen is very different. Seeing the black screen implies that we distinguish it from a grey screen, a red screen, a black table, a green house, a pink face, a dog, a sound, a feeling, or any other sensory event that would have been possible. Consciously seeing the black screen thus carries a huge amount of information, as it excludes an almost endless set of alternative sensations. And that makes seeing "that brown face of my sad-looking friend Peter" very different from what a face-selective neuron does when it signals "face". The neuron behaves much like the photodiode, in that it signals presence or absence of a feature along a single dimension. That is because neurons tend to combine feature-selectivity with invariance for other features: a face-selective cell signals faces regardless of colour, size, identity or expression (Rolls 1992).[14]

Tononi proceeds from a photo-diode to the photo camera as a metaphor for explaining another central feature of conscious sensations (2004, 2008, 2012). He argues that the critical difference between a conscious representation in the human mind and what happens in a camera is that in the camera information is distributed and not integrated. Each and every pixel signals a particular level of luminosity, but it does so entirely on its own. It does not "know" what other pixels are doing. To the camera it would not matter if all the pixels were cut apart and became separate cameras. Conscious sensations, on the other hand, are integrated.

It thus seems that to find for visual operations that are more closely linked to consciousness, we must look for something beyond basic categorization. We must look at processes where the individual pixels in our camera—the billions of neurons each signalling particular features—are interacting, and are integrating their information.

5 Interference: A loss of independence

The pixels in the "camera of the human mind" do not work independently. A strong case in point are illusory brightness or colour shifts. Patches of the exact same brightness may be perceived as entirely different, depending on their surroundings, and depending on the global configuration of brightness and contrast. A striking example is the cylinder with checkerboard illusion shown in the right half of figure 2. Similar illusions exist in the domain of colour (figure 2, left). Relatedly, everyone who has ever tried to paint a picture has experienced that it takes an astonishingly rich palette of reds, purples, browns, yellows, and even greens or blues to construe a veridical depiction of a simple red apple. The unitary experience of see-

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[13] Another illustration of the separation between feature selectivity and conscious experience is the observation that many neurons signal features of which we are not aware: V1 neurons signal the orientation of gratings that are of too finely spaced for us to perceive (He et al. 1996; Foster et al. 1985), respond to 3D disparity where we do not see depth (Cumming & Parker 1997), or signal invisible temporal frequencies (such as the flickering of light beyond the flicker-fusion frequency of about 15–25Hz, Maier et al. 1987).

[14] Responses are modulated by such features, but typically this happens only after some delay (Sugase et al. 1999). The initial feedforward response is typically fully governed by a basic feature, like face vs non-face. Later on, responses are modulated by face identity or expression, and this is mediated by horizontal or recurrent interactions between neurons. We then enter the domain of feature integration, which *is* a hallmark of conscious recognition; see below.

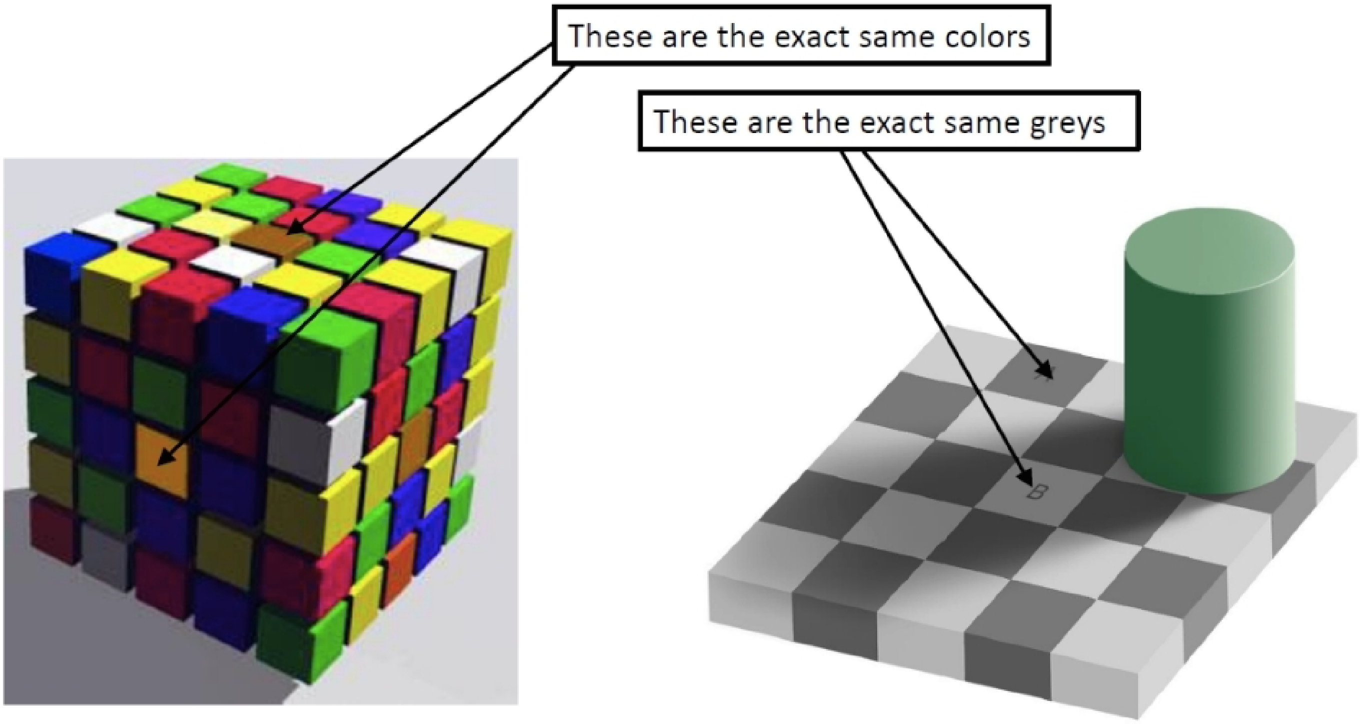

Figure 2: Two strong shifts in the perception of colour and brightness. Although the indicated patches are identical, they are perceived as having quite different colour and brightness. Visit Michael Bach's website (http://michaelbach.de/ot/) for these and many other examples.

ing a red apple is in fact composed of the detection of a multitude of wavelengths, all interacting to compose that one colour. Only with extreme focused scrutiny (or by covering surrounding elements) are we able to isolate the elements that make up our unitary conscious experiences.

Another illustration is the phenomenon of colour constancy. When we look at a bowl of fruit in the blue morning light the spectral composition of wavelengths reflected from the fruits is very different from the wavelengths coming from the fruits at sunset (figure 3). Nevertheless, we see the banana or the apple as having the same colour whether it is dusk or dawn. Our visual system is not interested in the wavelength coming from fruits; it is interested in their potential taste or edibility. Therefore, it discounts the illumination, and computes "colour", which is a property of the object, rather than of the light coming from it.[15] Colour is not wavelength; colour is a meaningful property of objects that is based on wavelengths, yet transcends it.

To what extent do these phenomena depend on consciousness? Harris et al. (2011) studied a brightness illusion much like that in figure 2. Two circles were shown, of either the same or different brightness. By placing these circles in a dark and bright surround respectively, their brightness suffered from an illusory shift. In the critical condition, the surrounds were made invisible by presenting them to one eye, and filling the other eye with a continuously flashing Mondrian stimulus. This resulted in CFS of the surrounds. Cleverly, the two circles were shown in both eyes, so remained visible throughout. Regardless of the CFS-induced invisibility of the surrounds, the circles still showed illusory brightness shifts.[16]

The neural mechanisms of illusory brightness perception were studied extensively

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[15] It probably discounts the illumination by very much the same mechanisms as the illusory brightness shifts discussed above (via inhibitory lateral interactions). However, precise neural mechanisms may be different, as might be the cortical level at which neural responses reflect colour rather than wavelength.

[16] It must be noted that in this experiment, the surrounds were not always fully invisible. In 86% of the trials, subjects reported not seeing the surrounds. Only these trials were used for the analysis. Within these trials, discrimination of the background (is the darker half left or right?) was at chance level, leading to the argument that indeed there was a full absence of awareness of the surround.

Figure 3: These images show a bowl of fruit photographed in three lighting conditions—artificial light (left), hazy daylight (middle), and clear blue sky (right). Notice the marked variation in colour balance caused by the spectral properties of the illuminant. We are not normally aware of this variation because colour constancy mechanisms discount illumination effects (image and legend from http://www.psypress.co.uk/mather/resources/topic.asp?topic=ch12-tp-04).

in the macaque monkey and cat visual cortex. It was found that perceived brightness (modulated by flanking regions) influenced neural responses in area V1 of the cat, but not at earlier stages such as the LGN or the optic tract, thereby showing a gradual progression from physical brightness to perceptual brightness in the visual pathways (Rossi & Paradiso 1999; Rossi et al. 1996). Using the Cornsweet brightness illusion,[17] it was found that in the monkey's visual cortex, V2 cells represents surface brightness whereas V1 cells do not, pushing the level at which perceived brightness is calculated somewhat higher (Roe et al. 2005). Either way, these results were recorded in anaesthetized animals, showing their independence from consciousness.

How the visual system goes from the detection of wavelength towards the representation of colour is still a topic of controversy. Initially, there was thought to be a modular progression from V1 cells encoding wavelength towards V4 cells encoding colour. That view was challenged by various findings showing that the responses of V1 cells are influenced by surrounding hues. The view that V4 is the "colour module" has also been challenged, in part by strong disagreement on the homology between monkey V4 and alleged human counterparts.[18] Moreover, the coding of colour is intricately linked to the coding of object shape, and hence can no longer be viewed as a simple "add-on" to our visual percept.[19] It is now thought that the perception of colour depends on the interaction between neuronal groups, or is best understood as a population code (Shapley & Hawken 2011).

Given this controversy, it is difficult to know to what extent colour perception depends on consciousness. Many of the recordings in monkey visual cortex were performed in awake animals, some in anaesthetized animals (Shapley & Hawken 2011). A clear-cut difference in results between the two conditions is hard to establish. A remarkable finding is that blindsight patients report no conscious sensation of colour, yet may have spectral sensitivity curves that have a similar shape in the lesioned and intact hemi-fields (Stoerig & Cowey 1989). Spectral sensitivity is, however, mostly carried by wavelength. Similarly, patients with cortical colour blindness (achromatopsia) do not consciously perceive colour, yet can detect objects or patterns based on wavelength contrasts (Cowey & Heywood 1997). Colour constancy mechanisms, on the other hand, are absent in the lesioned hemi-field of blindsight patients (Barbur et al. 2004; Barbur & Spang 2008), and

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[17] In this illusion, two surfaces of identical brightness are perceived as having different brightness, because there is a contrast edge between them.

[18] I am not even going to dare mentioning their names here.

[19] The fact that black-and-white photography works so well, has led us to believe that colour is a feature that is "painted" onto objects, as a sort of extra, independent of any other feature. We are now coming around from this view. For example, to compute the colour of an object, the object's shape has to be taken into account, otherwise shadings would be misinterpreted. Object identity also influences colour perception: a brownish colour on a banana will be seen as more yellow than it would on a tomato.

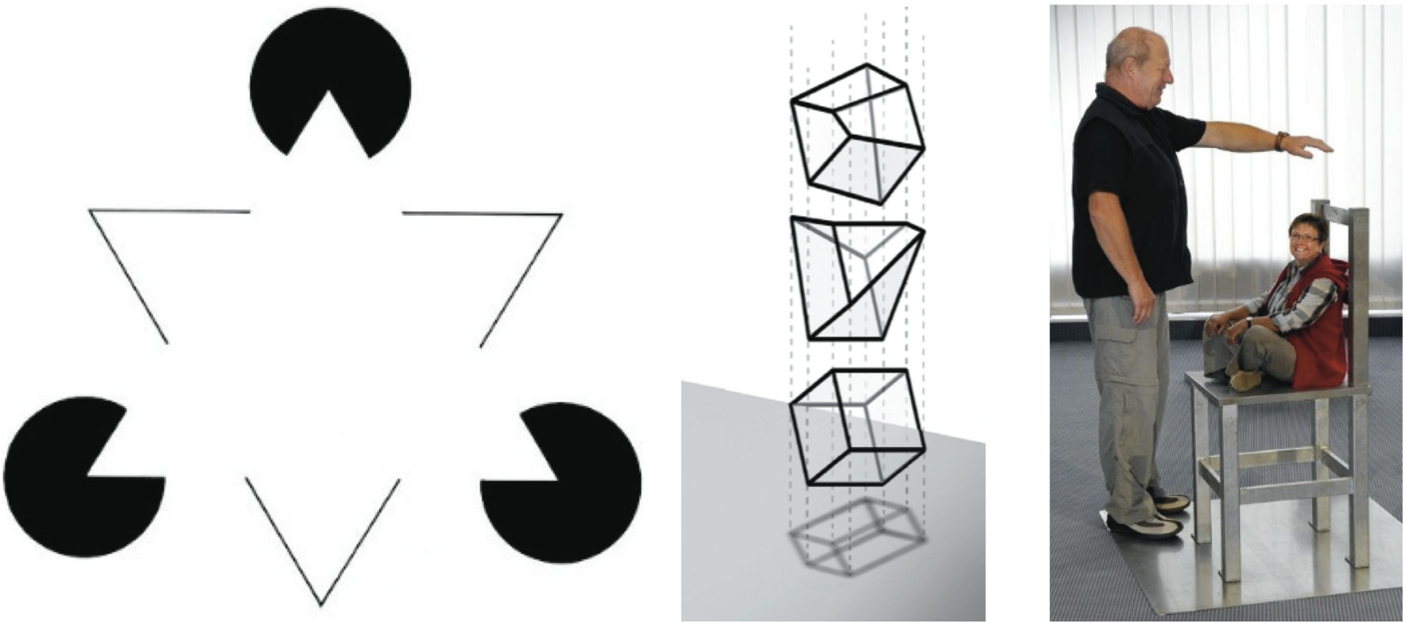

Figure 4: Left: the Kanizsa triangle. Note the illusory brightness increase inside the region of the illusory triangle. Middle: the 2D projection of a cube can in fact originate from a multitude of 3D objects. We regularly interpret it as a cube, however. Right: we see the woman as small, despite our cognitive ability to realize that “this cannot be true”. Our 3D “priors” force us to see her as small (from https://richardwiseman.wordpress.com/2009/09/09/great-table-illusion/).

hence seem more closely linked to conscious perception.[20]

The difference between perceived colour and wavelength, and its relation to conscious vision, has been directly addressed in a masked priming experiment. In this experiment, subjects were shown desaturated blue, green, or white coloured disks. Perceptually, the white was closer to the blue disk. From the point of view of the phosphor activations on the monitor screen, on which the disks were shown (i.e., their “wavelength composition”), the white disk was, however, closer to the green disk. What was studied was the effects of these disks when they acted as primes for a subsequent colour discrimination. It was found that masked, and hence invisible white disks, acted more like green primes than like blue ones. Visible white disks, on the other hand, acted more like blue primes than like green ones (Breitmeyer et al. 2004; Breitmeyer et al. 2007). Apparently, unconscious priming acts on wavelength similarity, whereas conscious priming acts on perceived colour similarity.

All in all, it remains difficult to assess the relation between consciousness and phenomena like brightness or perceived colour illusions, or mechanisms related to colour constancy. Perceived brightness seems to depend on largely unconscious mechanisms, and on fairly low level and short range mechanisms. The transition from wavelength analysis to the perception of colour is more likely to accompany the transition from unconscious processing to conscious vision. A firm conclusion, however, relies upon settling the debate about mechanisms of colour perception and their neural substrates in humans and animals, and more direct experimentation on how these mechanisms are affected by manipulations of consciousness.[21]

6 Inference: Beyond the input

In the phenomenon of colour constancy we have already seen a hint of another visual function.

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[20] This argument is, however, weakened by the fact that other long-range colour interactions remain in the blind hemi-field (Barbur et al. 2004), and by the finding that colour constancy mechanisms may depend on fairly early, monocular mechanisms (Barbur & Spang 2008). Moreover, it is reckoned that several colour constancy mechanisms exist, some of which are based on retinal adaptation mechanisms (Kamermans et al. 1998).

[21] Obviously, these empirical issues about colour perception and consciousness have very direct consequences for many philosophical debates as well, given the many thought experiments that rely on colour perception and the whole notion of qualia.

Colour is not about the wavelength coming from objects. It is a property of objects that we infer from wavelengths. At some point, conscious perception starts to diverge from the mere physical properties of the input, in a process we call *inference*. There are many more examples of inference, and many visual illusions capitalize on the fact that our visual mechanisms are constantly trying to make sense of the world. Figure 4 shows the famous Kanizsa triangle. The minimal, strictly physical interpretation of the image is that of three Pac men pointed at each other and three arrowheads pointing outwards. But our perceptual interpretation goes beyond this, in that we *see* a white triangle hovering over three black circles, occluding another outlined triangle. The illusory triangle is seen as slightly brighter than its surround, and illusory contours mark its "borders".

This process of inference seems to strongly fit the intuitive difference between a camera and conscious vision. It requires the integration of multiple "pixels", their interaction, and their interpretation beyond what is strictly given by the image itself. And it is in this last aspect in particular that prior knowledge about the world comes into play, and starts to interfere with the stimulus-driven feature-selective categorization of the input.

The Kanizsa triangle can be seen as a specific example of the more general propensity of the visual system to arrive at a representation of surfaces in 3D space (also called the 2.5D sketch). In that representation we seek the most natural interpretation, consistent with our existing experience of how things are in the world. It is simply much more likely that there is a triangle covering circles than that there are three Pac men that happen to be facing each other at exactly 60° angles. The triangle interpretation is generic, whereas the Pac men one would be accidental (Albert & Hoffman 2000). Nakayama & Shimojo (1992) studied various configurations of 3D stimuli, and found that our visual system always strives towards the interpretation that is most generic, i.e., that would least depend on an accidental viewing position of the observer. Interpretations that would not change when the observer happened to shift position are favoured, given that we are constantly moving relative to objects. For example, the 2D image of a cube can in fact arise from an infinite number of shapes (figure 4, middle), yet we tend to favour the "cube" interpretation because it is the most generic one.

Another way of putting it would be to say that the cube interpretation fits our common experience, in that most of the time, these kinds of 2D projections arise from regular 3D cubes: it is the most ecologically valid interpretation. In a modern guise, this aspect of inference is formalized as a Bayesian approach, where vision uses a set of prior probabilities to arrive at the most likely 3D interpretation of a 2D image. The cube has the highest prior, compared to the more irregular shapes. Illusions like the Ames room (where someone changes size when he walks from one corner to the other), or the size illusion shown in figure 4 (right) capitalize on these assumptions: we assume that rooms have rectangular floors and walls, we assume the woman is sitting on a chair. These assumptions are so strongly embedded in our visual hardware that even in the face of strange consequences, such as people growing in size within a few steps or a man holding his hand over a mini-woman, this inference is maintained.

Many more illusions display non-veridical inferences. In the Ebbinghaus illusion, the perceived size of a disk depends on the size of surrounding disks. In the Ponzo and Müller-Leyer illusions we see line segments as having different lengths, while in fact they are the same. These illusions show that the size of an object is an inference that we draw from its context, rather than from the space it occupies on the retina.

To what extent does inference depend on conscious vision? When we have to pick up the disks in the Ebbinghaus illusion, it appears that our hands open at a pre-grip aperture that is in accordance with the disk's actual size, not its perceptual size. Apparently, size context effects influence perception, and not automatic action—which has led to the idea that we have two largely separate neural pathways, one transforming visual input into conscious perception, and the other translating visual input into automatically guided action (Goodale & Milner 1992).

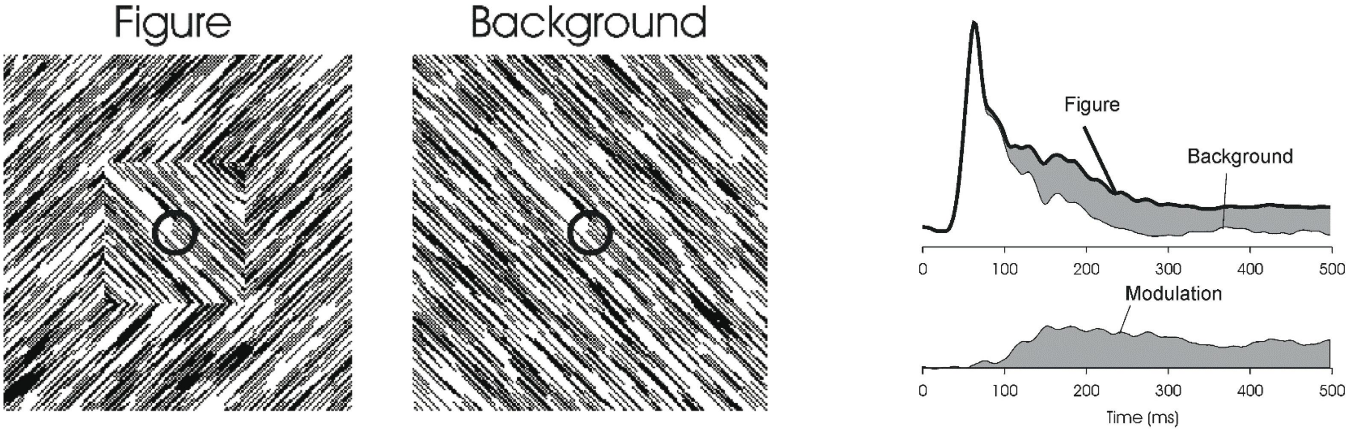

Figure 5: On the left, we see a textured square overlying a textured background. This is because we automatically group all line segments with the same orientation into one object, and segregate it from the line segments with the orthogonal orientation. The small circle represents the receptive field of a V1 neuron, that would not be able to differentiate between the "figure" and the "background" stimulus, because the line segments within that receptive field are identical. Indeed, V1 responses are identical up to about 100ms after stimulus onset. Beyond that, the two responses start to diverge, however, indicating that the response of the V1 neuron is modulated by the perceptual context of what is within its receptive field (Lamme 1995; Lamme et al. 2000).

There is more evidence linking perceptual inference to conscious vision. Harris (Harris et al. 2011) studied whether Kanizsa triangles were still inferred when the inducers were made invisible using CFS. The same setup was used that showed the presence of brightness illusions under CFS (see above). Subjects had to indicate whether the triangle in the suppressed eye was pointing left or right. They were at chance level, indicating that the Kanizsa-type inference depends on consciousness. Another study, however, found that Kanizsa triangles broke through CFS earlier than control stimuli with inducers pointed outwards (Wang et al. 2012), suggesting that Kanizsa-type inference does occur pre-consciously.

At the single neuron level, the detection of illusory contours has been studied quite extensively. Initially, it was found that V2 cells respond in an orientation-selective manner to Kanizsa-type illusory contours (Von der Heydt et al. 1984). More recently, other areas have been shown to be involved as well (Sáry et al. 2008)—area V4 in particular (Cox et al. 2013). And in human neuroimaging studies it was found that Kanizsa-type illusory contours activate many early visual areas (Seghier & Vuilleumier 2006). All these studies used awake animals or humans, so it is difficult to infer whether these responses depend on the conscious state.

Marcel studied the processing of illusory triangles in two blindsight patients. Two inducers were presented in the sighted hemi-field, while one critical inducer was presented in the blind field, either completing the triangle or not. Completed triangles were detected far above chance (~80%), while the detection of the inducer shape was at chance. Moreover, one of the subjects described the illusory triangles as "brighter", "out there on the screen" and "on top of something" (Marcel 1998).

All in all, the relation between inference and consciousness is unclear, mostly because fairly little work has been done as yet to study the relation directly (i.e., to study the effect of consciousness manipulations on inference and its neural correlate), but also because much of the work that has been done focuses on a single (though very important) phenomenon: the Kanizsa triangle.

7 Integration: Feature grouping and segregation

Both in interference phenomena such as brightness or colour shifts and in inference phenomena like the Kanizsa triangle we see some aspects of the integration of information. Visual responses go beyond the encoding of individual pixels, and start to influence each other, either on the basis of more or less hardwired lateral interactions, or on the basis of the incorporation of prior knowledge. In the end, conscious vision seems to be about reaching *full* integration.[22] We have one visual percept, where all information is combined.[23] This is a property of conscious vision that has interested scientists for a long time. Gestalt psychologists formulated a multitude of laws, along which image elements may be combined into larger wholes (Rock & Palmer 1990; Wagemans et al. 2012). In this grouping process, all features, together with their interactions, inferences, and meanings are combined into a final percept: the thing we see, the whole scene containing shapes, objects, and backgrounds. This is a highly dynamic process in which various Gestalt laws may compete for one interpretation or another, and where subtle changes may influence the meaning of pixels at long distances. We enter the domain of feature integration, grouping, binding and segregation. In short; the domain of perceptual organization.

Two levels of integration may be distinguished, where a subdivision between “base groupings” and “incremental groupings” may be useful (Roelfsema 2006). Base groupings are those that depend on the fact that some feature combinations automatically ride together. An orientation-selective cell in the primary visual cortex, for example, is often at the same time also direction-selective. It may be tuned to particular binocular disparities as well. And it will have a limited receptive field. So the firing of that neuron already goes beyond a one-dimensional feature-detector, beyond the photo-diode. It signals an orientation, moving in a particular direction, at a particular 3D depth, and located in some part of the visual field. Such base groupings exist for many feature combinations, such as colour and shape (e.g., V4 cells), or motion and disparity (e.g., middle temporal, MT, cells).

Another type of base grouping is visible in the feature selectivity of a particular cell, where we may recognize the combination of feature-selectivity of cells at earlier levels. From the start, Hubel and Wiesel recognized that orientation selectivity could be viewed as a convergence of information from retinal ganglion cells lying in a row. The feedforward convergence of information from orientation selective simple cells leads to the receptive field structure of complex cells, which are orientation and direction selective (Hubel & Wiesel 1968). Many higher-level feature-selective cells can be seen as converging information from lower level cells (Tanaka 1996).

Base grouping does not depend on consciousness. The combined feature selectivity of neurons, as well as high-level feature selectivity based on the feedforward convergence of lower-level feature selectivity are still present in anaesthesia or masking (Lamme & Roelfsema 2000; Roelfsema 2006).

Of a very different nature are “incremental groupings”. Here, the information from separate neurons has to be combined to obtain a higher level categorization. A good example is texture based figure-ground segregation, shown in figure 5 (Lamme 1995; Zipser et al. 1996). Here, we automatically perceive a textured square overlying a textured background. This is entirely due to the fact that the centre square is made up of line segments of a particular orientation, different from the line segments that make up the background. There is no luminance difference or any other cue that gives the square “away”. Line segments of one orientation are automatically grouped into a coherent surface—the square—that is segregated from the surface that is

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[22] Tononi similarly argues that consciousness always strives for “maxima of integrated information”, for which he uses the metaphor of the internet (2012). Like the brain, the internet is a highly interconnected structure where information travels from one part to other parts. In contrast to the brain, however, the internet is designed to transfer information from one specific part of the net (computer A) to a specified other part of the net (computer B), and it would in fact be rather counterproductive if this information were influenced by other information flowing from computers C to D or E to F. At another moment information may flow from A to C or D or F. The internet therefore does not strive for “maxima of integrated information”, whereas the brain typically does. Focussed attention, in such a view, would then be in fact a mechanism that counters this propensity towards maximally-integrated information, and which enables the brain to operate more strongly along the principles of the internet.

[23] This is in fact such a strong intuition that it has led us to believe for a long time that consciousness must be some place in the brain “where it all comes together”. Descartes envisaged the pineal gland as such a place, and hence theories that lean towards such an explanation of consciousness are often said to suffer from the fallacy of the “Cartesian theatre”.

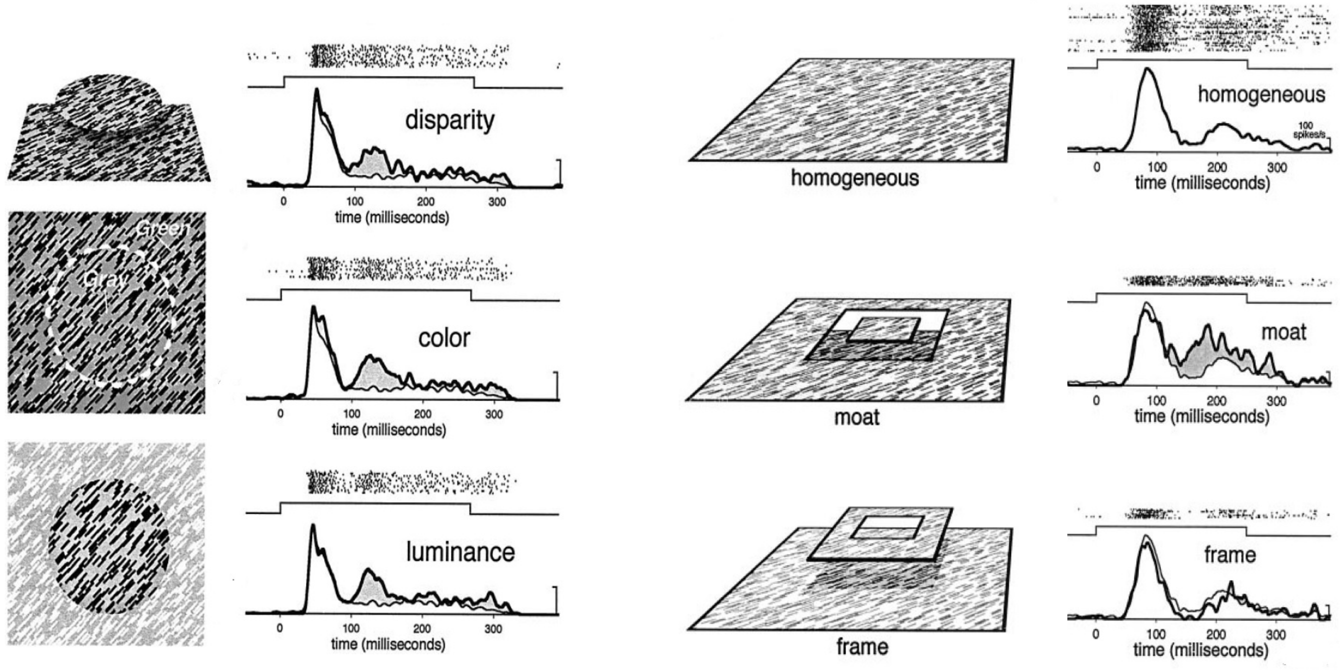

Figure 6: Contextual modulation of V1 responses follows the global perceptual interpretation of images. In all cases, the V1 receptive field is stimulated with the exact same line segments. When these line segments belong to a homogenous background texture, a response indicated by the thin line is given. Left: when the line segments belong to a figure that is defined by differences in disparity, colour, or luminance, the responses are larger. Right: differences in 3D disparity were used so that the patch of texture was either part of a figure square "floating in a moat behind it" or in the background with a "frame" hovering in front of it. The contextual modulation always followed these perceptual interpretations, in that "figure" interpretations always evoked larger responses (Zipser et al. 1996).

formed by line segments of the other orientation —the background. Orientation-selective neurons in V1 typically have small receptive fields, which would only cover a small part of either the figure or background. The grouping of line segments into coherent surfaces, segregating from each other, requires the integration of information from a large set of separate V1 cells. This constitutes "incremental grouping" (Lamme & Roelfsema 2000; Roelfsema 2006).

The neural basis of the integration of image elements into larger units, and the subsequent segregation of such units into figure and ground has been studied extensively at the single unit level, both in anesthetized and awake monkeys. The key finding is that of "contextual modulation", where the response of a neuron to a particular feature within its receptive field is modulated by the larger perceptual context of that feature (Lamme 1995; Zipser et al. 1996; Lamme et al. 1999). In the example of figure 5, the small circle represents a V1 receptive field, which typically has a size of ~1 degree of visual angle. From the "point of view" of that receptive field, there is no difference between the "figure" or the "background" stimulus: in both cases, identical line segments cover the receptive field, and if the neuron were just signalling the presence of this feature ("left diagonal orientation present"), the responses of this neuron should be identical for the two stimuli. Indeed they are, as shown in the panel on the right, showing fully overlapping responses, until ~100 ms after stimulus onset. At that point, however, the responses for figure and background start to diverge. Apparently, information on the context of the line segments starts to influence the response, so that the response is larger for the "figure" than for the "background" context (Lamme 1995).

These kinds of figure-ground modulations follow the perceptual interpretation of scenes to a large extent. For example, when figure-ground relationships are ambiguous, or reversed, the

Figure 7: Contour grouping. In all cases shown here, oriented image elements are grouped together to form either a line (left), a circle (center), or an animal (right). They group according to the Gestalt principles of proximity, similarity, and colinearity. These stimuli were also used in neurophysiological experiments, typically showing that elements that group and segregate evoke larger neural responses than isolated or background elements.

modulation follows the globally-organized percept, rather than local orientation differences or gradients (figure 6, right panel) (Zipser et al. 1996; Lamme & Spekreijse 2000).

The perceptual grouping of image elements into larger units follows certain rules and principles, the formulation of which was the largest contribution of the Gestalt psychologists to modern vision theory (Wagemans et al. 2012). Among these Gestalt laws of perceptual organization are “similarity” (elements that look alike will be grouped), “common fate” (elements that go together in time, e.g., move together, will be grouped), “proximity” (elements that are close together will be grouped), and “good continuation” (elements that lie along a smooth line will be grouped). Contextual modulation of V1 neurons behaves according to these rules, in that elements that share luminance, colour, disparity, orientation, direction of motion, or co-linearity induce facilitatory interactions (figure 6 & 7) (Lamme et al. 1993; Lamme 1995; Kapadia et al. 1995; Zipser et al. 1996; Lamme et al. 2000).

How does Gestalt grouping and segregation depend on consciousness? To some extent, contextual modulation seems to survive during anaesthesia. This is, however, largely limited to fairly short range interactions between neurons, barely beyond or entirely within the receptive field (Allman et al. 1985; Gilbert & Wiesel 1992; Nothdurft et al. 1999). More long-range interactions, and interactions that express more global scene interpretations can only be recorded in awake monkeys (Knierim & Van Essen 1992; Lamme 1995; Kapadia et al. 1995; Zipser et al. 1996). For example, the figure-ground specific modulation of V1 responses shown in figures 5 and 6 (and structure from motion defined figure–ground modulation) is fully absent when monkeys are anaesthetized. At the same time, the orientation and motion selectivity of these neurons (i.e., their ability to categorize certain features) is not affected at all (Lamme et al. 1998a).

Similarly, backward masking disrupts figure–ground modulation. In monkeys, the visibility of texture orientation defined figure-ground targets was manipulated by masking with a stimulus consisting of randomly-positioned texture-defined figures (figure 8). The animals were at chance in detecting the location of the target figure for stimulus-onset asynchronie (SOA) of up to 50 ms (i.e., 50 ms between the onset of the target figure and the mask). At larger SOA’s, behaviour quickly rose to ceiling. Figure-ground contextual modulation followed the same pattern: absent up to and including SOA’s of 50 ms, and increasingly present at longer latencies. At the shorter latencies, however, V1 neurons still responded vigorously to the texture patterns in an orientation-selective manner,

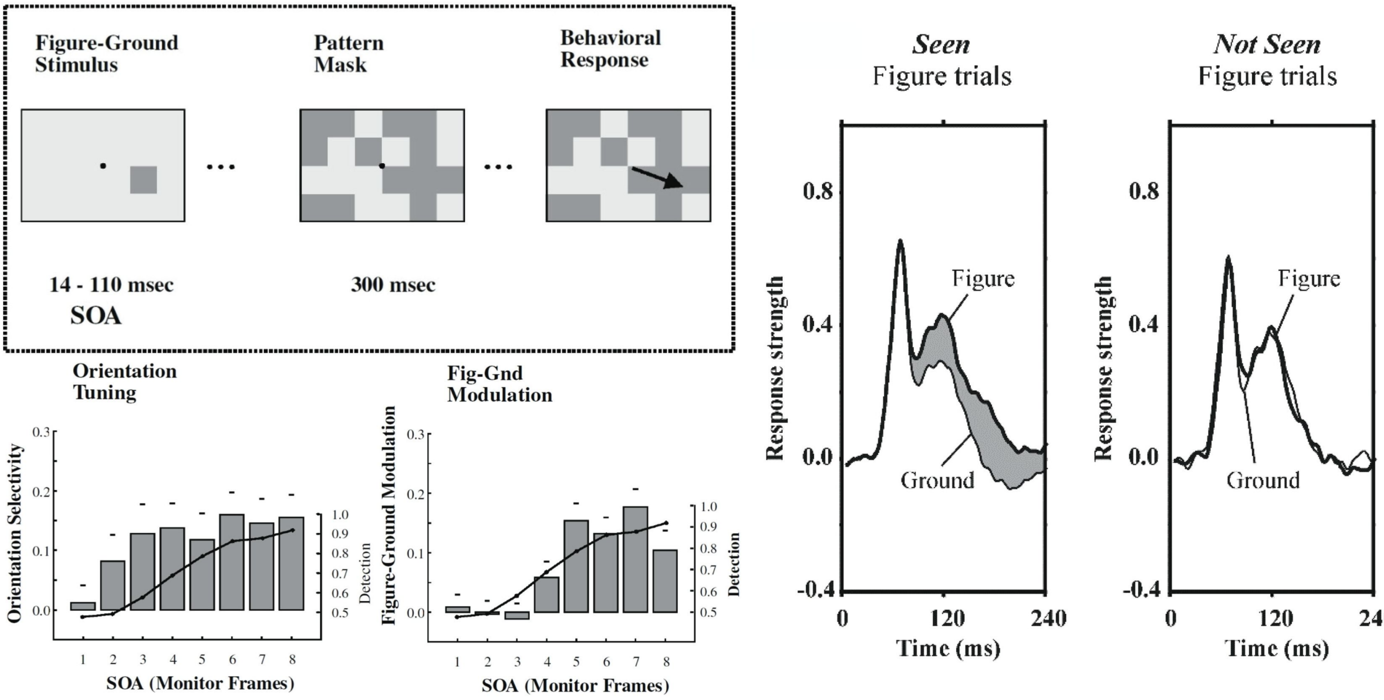

Figure 8: Left, above: textured figure-ground squares (like shown in figure 5) were presented either left or right of the fixation spot, and monkeys had to indicate their position with an eye movement. The figure targets were masked with a pattern of randomly-positioned texture squares. Left, below: the graphs show—for different SOA's—the ability of monkeys to correctly identify the position of the squares (line graph) versus the strength of either orientation-selective responses or figure-ground modulation (bars). Monkeys do not see the figures at SOA's of up to 3 frames (~50ms), and likewise, contextual modulation is absent in those cases, whereas orientation selectivity is not (Lamme et al. 2002). Right: monkeys had to indicate the presence or absence of textured figure targets by making an eye movement or deliberately maintaining fixation. When figures were not seen, contextual modulation was absent (Supèr et al. 2001).

showing that lower level classification was still present for unseen orientations (Lamme et al. 2002). Similar results were obtained in human subjects using EEG responses (Fahrenfort et al. 2007).

Contour grouping, as displayed in figure 7, is particularly susceptible to masking. When these displays are temporally alternated, so that each element rotates 90^0 in successive displays, a strong masking effect is observed.[24] Depending on the angle between elements forming a contour, visibility drops to chance at alternation frequencies between 12 and 1Hz. This implies that the integration of these contours takes between 80 to 1000 ms (Hess et al. 2001).

Zipser used dichoptic masking to render orientation-defined figures invisible. Figure-ground stimuli like those of figure 5 were shown to the two eyes of awake and fixating monkeys, yet with opposite orientations in either eye. As a result, the dichoptically-fused image consisted of cross-like elements, in which a figure was no longer visible.[25] Figure-ground modulation was absent in this case (Zipser et al. 1996). In a similar experiment in human subjects, Fahrenfort used face stimuli that were defined by oriented texture differences. A face was present in each image presented to the two eyes. Yet when binocularly combined, the face disappeared in the fused percept. He compared the neural signals obtained for such stimuli to responses to similar stimuli where binocular fusion resulted in a vis-

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[24] This manipulation is a combination of backward and forward masking, and also somewhat reminiscent of dichoptic masking, in that in subsequent displays images with the opposite orientation contrast are shown. See the two images of figure 9, but then not presented to the two eyes but in rapid alternation.

[25] A similar setup was used in the curious case of alleged “blindsight in normal observers”. In one of the experiments in that paper, target figures were made invisible using the same manipulation of dichoptic presentation of orthogonally-oriented elements. It was claimed that despite their subjective invisibility, subjects were able to localize the targets above chance, just as blindsight patients do for unseen stimuli (Kolb & Braun 1995). The findings were not replicated, however (Robichaud & Stelmach 2003).

ible face (figure 9) (Fahrenfort et al. 2012). A striking finding was that visibility (although rigorously checked behaviourally) had no effect on the ability of the Fusiform face area to distinguish between face and non-face stimuli, once more corroborating the independence of categorization responses and consciousness. In addition, invisible face stimuli could be classified from neural responses when training the classifier on visible stimuli and vice versa. The difference between visible and invisible binocular faces was found in the fact that visible faces evoked strong recurrent interactions between the FFA and earlier visual areas, both expressed in the fMRI signal (assessed using psycho-physiological interaction analysis with the FFA as a seed), as well as in the EEG signal (showing a larger amount of theta, beta and gamma synchronization, and the presence of figure-ground modulation only in the visible condition).

The most direct relation between contextual modulation and consciousness was perhaps demonstrated by Supèr et al. (2001). Monkeys were shown oriented texture figure-ground targets at different locations, and had to signal their presence by making an eye movement towards their positions. Importantly, however, in 20% of the trials, no figure was presented at all, and the monkeys had to maintain fixation on those catch trials for the duration of the stimulus.[26] Indeed the monkeys refrained from making eye movements on catch trials (as they were trained to do). But also on some 8% of trials in which a figure *was* presented they maintained fixation, as if to say "I did not see a stimulus here". There was a striking difference in the level of contextual modulation for seen versus not-seen figure targets: modulation was fully absent for not-seen figures (figure 8). Seemingly, on some trials contextual interactions spontaneously fail to develop, and the result is that figure targets were invisible.[27]

That brings us to the question of neural mechanisms. Seemingly, the visual functions of perceptual organization, grouping according to Gestalt laws, and figure-ground segregation all depend strongly on the conscious state, and on the objective (or subjective) visibility and perceptual interpretation of the stimulus. Do these functions have similar neural mechanisms? There has been much debate on the neural connections underlying contextual modulation effects. Given the latency of the effects (typically several milliseconds after the initial categorization or feature response) it was originally hypothesized that they depended on feedback signals from higher-level visual areas (e.g., V4, IT, MT, etc.) toward lower levels (e.g., V1, Zipser et al. 1996). Experiments using cooling or lesioning of higher-level areas gave mixed results. Local inactivation of V2 using GABA injections had no effect on short- to medium-range contextual effects in V1 (Hupé et al. 2001). Cooling area V5/MT, on the other hand, had effects on figure-ground signals in V1, V2, and V3 (Hupé et al. 1998). These effects, however, worked on the early part of the response, and were evoked using stimuli where segregation depended more on contrast differences than on the long-range integration of information (Bullier et al. 2001). Others also found figure-ground effects that were faster than those discussed here (Sugihara et al. 2011). There is thus a whole range of contextual effects, some of which are faster than others, and some of which may depend on feedback while others do not.

There is one counterintuitive aspect of interpreting these results in this way: in fact, feedback connections are not slow, but just as fast as feedforward connections, where both are at about 3.5 m/s (Girard et al. 2001). Horizontal connections that run via unmyelinated fibres in layers 2 and 3 of the cortex are about 10 times slower (Sugihara et al. 2011). Many of the Gestalt principles of perceptual organization

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[26] This paradigm has been shown to distinguish between seen and not-seen stimuli in monkeys with a V1 lesion in one hemi-field, and was used to differentiate between "conscious" visual responses and unconscious blindsight behaviour: without catch trials (i.e., when in forced choice mode), monkeys react to both stimuli in the intact and in the lesioned field, expressing blindsight capabilities. In catch trials, however, monkeys only respond to stimuli in the intact and not in the lesioned hemi-field, as if expressing conscious sensation instead of a mere reflex (Moore et al. 1995). Supèr et al. used the same paradigm in intact monkeys to assess conscious percepts of figure–ground stimuli.

[27] A later investigation into neural activity preceding either seen or not-seen figure trials showed that not-seen trials are preceded by somewhat lower level of spontaneous activity, and also express less inter-neuronal synchrony (Supèr et al. 2003; Van der Togt et al. 2006).

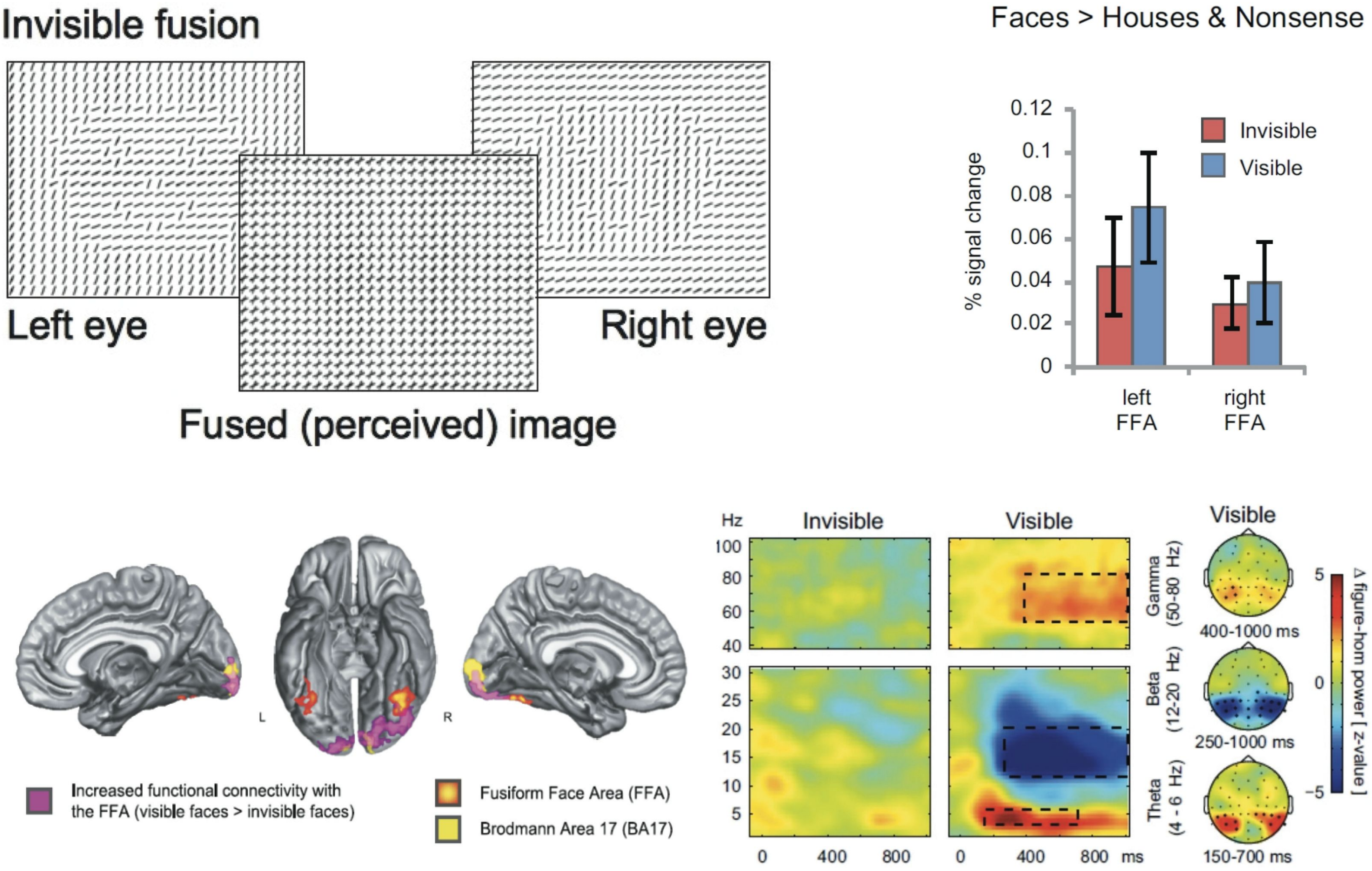


Figure 9: Top left: texture-defined faces were presented in either eye of subjects, yet with different orientations of line segments. As a result, the face was not visible in the fused percept (compare manipulation of figure 1). By using other orientation combinations, the same design could also result in a visible face (not shown). Top right: category-specific responses in the FFA did not differ for visible or invisible faces. Below: visible faces are characterized by strong recurrent interactions between FFA and earlier visual areas (left), and by strong synchronous activity in the theta, beta, and gamma bands (right). From: Fahrenfort et al. (2012).

are, however, embedded in these slow horizontal connections: V1 cells with a similar orientation preference are selectively interconnected via so-called patchy horizontal fibres. Moreover, these interconnections are strongest for oriented cells that have their receptive fields aligned along their orientation preference. Horizontal connections are also strongest between nearby cells (Gilbert & Wiesel 1989; Malach et al. 1993; Bosking et al. 1997). As such, these horizontal connections thus form the neural substrate of the well know Gestalt rules of “similarity”, “co-linearity”, and “proximity”. A similar arrangement of preferred interconnectivity has been found for motion-direction selective cells in MT (Ahmed et al. 2012), potentially forming the substrate of the grouping principle of “common fate”. Neurophysiological correlates of these grouping principles are relatively fast, however (Knierim & Van Essen 1992; Kapadia et al. 1995).

The figure-ground segregation effects of figures 5, 6, 7, and 8 are among the longest latency contextual effects reported. That may be because they depend on both horizontal and feedback connections. Figure 10 shows the result of an experiment where the complete peristriate belt of visual cortex surrounding V1 and V2 was subjected to suction lesioning, removing (parts of) areas V3, V3A, V4, V4t, MT, MST, FST, PM, DP, and 7a (Lamme et al. 1998b; Supèr & Lamme 2007). Before the lesion, an oriented texture figure–ground stimulus evoked elevated activity in all neurons responding to the figure elements. Response modulation was even somewhat stronger, and occurred earlier at

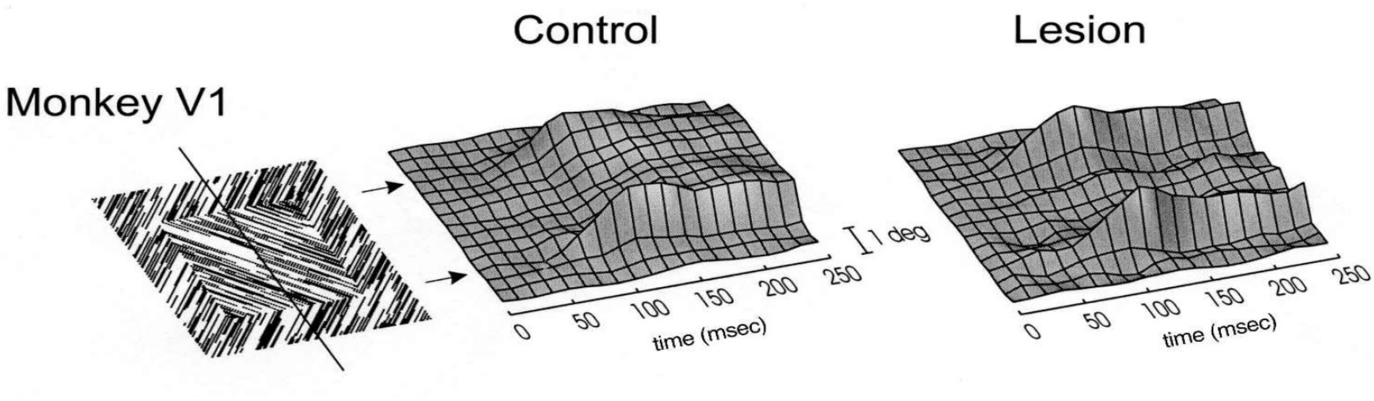
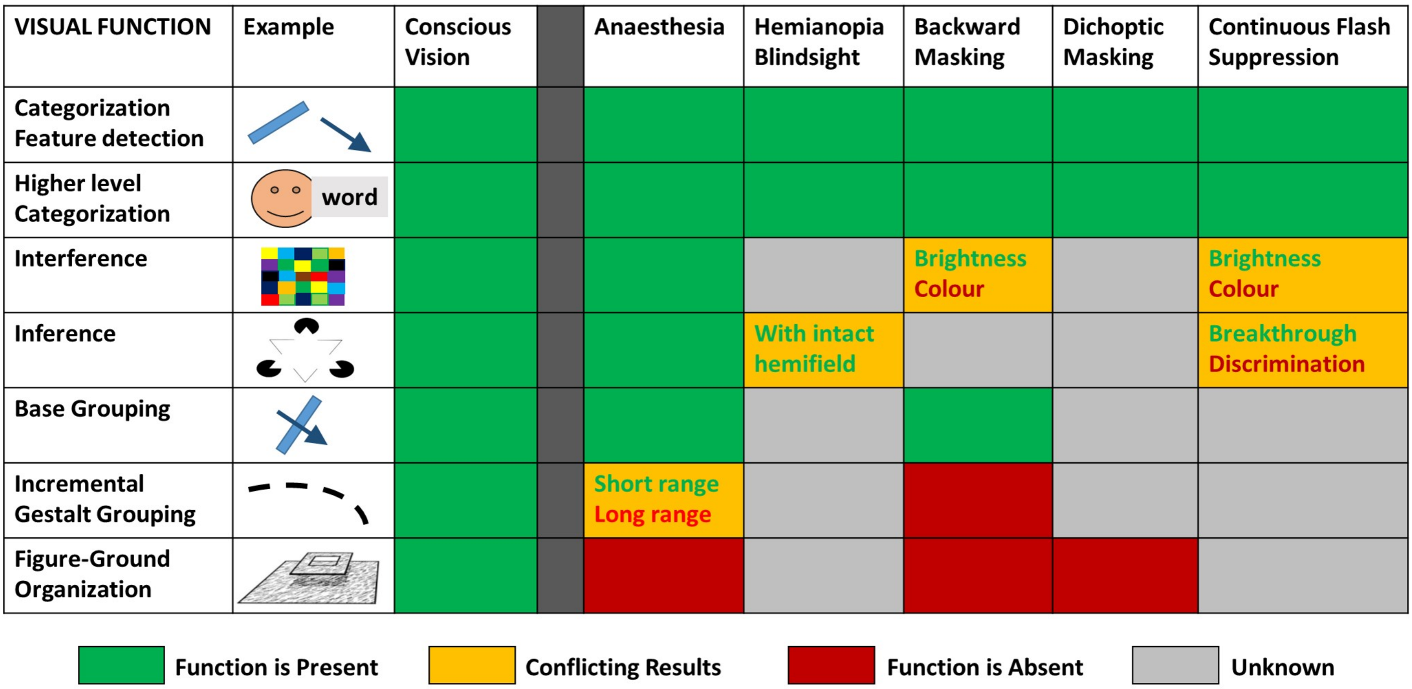


Figure 10: Contextual modulation (i.e., figure–ground responses, see figure 5) for various positions of the receptive field of V1 neurons (vertical axis), and extending over time (horizontal axis). In an intact monkey, modulation arises first at the figure-ground boundary, followed by a "filling-in" of the boundaries. After a lesion to the peri-striate belt of the visual cortex, only the boundary modulation remains, while filling-in has been abolished (Lamme et al. 1998a).

the boundary between figure and background. This was followed by a sort of "filling in" of enhanced activity between the boundary regions. We thus see an incremental process, starting with boundary segmentation and followed by surface segmentation. Similar findings have been reported in humans using combined EEG and TMS (Wokke et al. 2012).

After the lesion, the boundary enhancement remained, which may indicate that texture boundary detection mechanisms do not depend on feedback from higher visual areas and hence are mediated by horizontal connections within V1, or by recurrent interaction with V2. The centre modulation, where the figure elements are "neurally elevated" from the background elements, was completely abolished after the lesion, indicating that these figure-ground signals do depend on recurrent interactions between V1 and higher-tier areas. This finding was modelled on a realistic neural network of spiking neurons, indeed formalizing the idea that local orientation contrast—and hence the boundary between figure and ground—is mediated by inhibitory horizontal interactions between oriented receptive fields, whereas the figure–ground signal depended on excitatory feedback interactions trickling down from higher to lower areas (Roelfsema et al. 2002). Recently, laminar recording of figure-ground signals in V1 confirmed this idea (Self et al. 2013). These results show that the long-latency figure-ground segregation effects depend on incremental interactions mediated by both horizontal and feedback connections. That may be the reason why they are most vulnerable to anaesthesia, masking, and other manipulations of consciousness.

Tononi modelled several neural architectures in order to find the connection parameters that fulfil the requirements for achieving maximally-integrated information. The optimal architecture consists of neurons that each have specific and different connections patterns, yet are sufficiently interconnected for each neuron to be able to connect to another via a few steps. Uniformly, or strictly modularly organized networks are less optimal. The thalamo-cortical system fits these requirements very well. On the one hand, neurons should be interconnected, otherwise information is not integrated. On the other hand, too much interconnection leads to a loss of specific information, as all neurons start doing the same thing, which happens in epilepsy or deep sleep—states that are indeed accompanied by a loss of consciousness (Tononi 2004, 2008, 2012). The contextual modulations that have been explored here seem to exactly express these properties: on the one hand, the neural responses are very specific, in that the major part of the response is driven by the features that are within the (small) receptive field. But on the other hand, the integration of these



VISUAL FUNCTION	Example	Conscious Vision		Anaesthesia	Hemianopia Blindsight	Backward Masking	Dichoptic Masking	Continuous Flash Suppression
Categorization Feature detection		🟩		🟩	🟩	🟩	🟩	🟩
Higher level Categorization	word	🟩		🟩	🟩	🟩	🟩	🟩
Interference		🟩		🟩	⬜	🟨 Brightness Colour	⬜	🟨 Brightness Colour
Inference		🟩		🟩	🟨 With intact hemifield	⬜	⬜	🟨 Breakthrough Discrimination
Base Grouping		🟩		🟩	⬜	🟩	⬜	⬜
Incremental Gestalt Grouping		🟩		🟨 Short range Long range	⬜	🟥	⬜	⬜
Figure-Ground Organization		🟩		🟥	⬜	🟥	🟥	⬜

🟩 Function is Present 🟨 Conflicting Results 🟥 Function is Absent ⬜ Unknown

Figure 11: Table summarizing the influence of consciousness manipulation on various visual functions. Colours indicate whether functions (rows) still operate under aa particular manipulation (columns). In the case of conflicting or uncertain evidence (yellow), the cases or conditions where the function still seems present is written in green; the cases where the function is absent are written in red. All functions are assumed to be present in conscious vision. For each visual function, an icon depicts its most prominent example. See text for explanation.

features rides on top of that response as a moderate modulation, expressing perceptual integration that may cover a large spatial extent, yet never even beginning to fully override the information carried by the neuron. In other words, visual neurons have categorization as their main priority, yet they also integrate these categories at some point in their response. That is the moment in time where the seed for conscious perception is laid (Lamme 2003, 2006, 2010a, 2010b).

8 Is there a functional boundary between unconscious and conscious vision?

I have taken the two extreme ends of consciousness manipulation: clear-cut visible and above-threshold items in awake subjects veridically reporting their visual experiences versus visual processing in anaesthesia, blindsight, or during profound masking or suppression (figure 11). If we don’t accept conscious vision in the former, and the absence of it in the latter, there is no use arguing about the phenomenon of consciousness. Even so, it has been surprisingly hard to find fundamental differences in the workings of many visual functions in the two conditions. Categorization of visual stimuli, even up to high levels, clearly stands independent of conscious visibility. It is unclear whether interference—i.e., the fact that features are no longer treated independently—depends on consciousness: shifts in brightness perception do not depend on consciousness, while it is uncertain whether the transition from wavelength to colour perception (and colour constancy) marks the conscious-unconscious divide.[28] Similarly, the status of inference phenomena like those observed in the Kanizsa triangle is uncertain.

This is all the more surprising given that many of these functions have traditionally been viewed as expressing the transition from merely physical features detected by sensor arrays towards the perceptual interpretation of this in-

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[28] Yet this transition may be the “Holy Grail” for those willing to understand qualia—or at least for those believing in “soft qualia”, i.e., phenomenal properties that are not entirely detached from visual functioning, and having some sort of neural substrate (Block 1996, 2005, 2007).

formation. Moreover, they mark the integration of stimulus-driven input with our knowledge of the world, such that we arrive at visual "meaning". Recently, there has been quite some interest in so called predictive coding frameworks of vision (Rao & Ballard 1999; Panichello et al. 2012). In these frameworks, vision is seen as a type of Bayesian inference, where our prediction (prior) of the outside world is continuously matched with our sensory input, and where the difference is propagated through the network as an "error signal", which then results in an updating of the model (posterior). Indeed, expectations bias our perception of the world, most strongly in the face of ambiguous stimuli, but also in the case of unambiguous stimuli (Panichello et al. 2012). Although it has been suggested that either the matching process, the prior, or the posterior in this type of inference have some relation to consciousness,[29] this is questionable given the automaticity of many expectation effects. For example, the mere statistical dominance of a particular stimulus type is sufficient to bias perceptual interpretations (Chopin & Mamassian 2012). Also, expected words break from continuous flash suppression sooner than unexpected words (Costello et al. 2009).[30]

All in all, the relation between consciousness on the one hand and categorization, interference, and inference processes on the other hand ranges from non-existent to weak. A much stronger case seems possible for functions like the grouping of image elements according to Gestalt laws and figure-ground segregation. These operations seem to depend strongly on the conscious state, and on conscious perception of the stimuli involved (figure 11). This is surprising, given their relative "simplicity". For example, the grouping of similarly-oriented or collinear line segments may be achieved by horizontal connections in the primary visual cortex (Bosking et al. 1997, see above). Figure–ground segregation—and its neurophysiological correlate—has been successfully modelled in a recurrent network architecture consisting of orientation-selective visual neurons in three hierarchically-organized visual areas, combined with some inhibitory horizontal interactions and excitatory feedback (Roelfsema et al. 2002). Regardless, the experimental data clearly show that if we want to identify visual functions that mark the transition from unconscious processing to conscious vision, grouping according to Gestalt laws (incremental grouping) and figure-ground segregation[31] (or perceptual organization in general) are our best bets.[32]

9 Is it all about distance, or time?

So why do Gestalt grouping and segregation bear such a close relation to consciousness? From a neural perspective, they differ from most other functions in that they depend on interactions between neurons at rather large distances. For example, for a neuron to "know" whether it sits on the figure or the background of the stimulus in figure 5, information has to travel over a distance of about 20 millimetres in the visual cortex.[33] Moreover, the modulations of neural activity that accompany this "knowing" depend on the incremental push-pull interactions between horizontal and feedback connections (Lamme & Roelfsema 2000; Roelfsema et al. 2002; Roelfsema 2006). These require quite extensive processing steps, given that the con-

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[29] In my reading, the predictive coding models are sometimes rather vague about exactly which signal mediates conscious experience. It is often seen to be a combination of the matching process and the posterior, e.g., Seth et al. (2011).

[30] But note that this is in fact nothing more than a semantic priming experiment. The results primarily show that if a semantic category has been activated, this category will then break earlier from CFS.

[31] Of course one could argue that in the case of a face on a blank background there also is figure–ground segregation. This type of segregation clearly does not depend on consciousness. This touches on the debate on whether categorization is possible without segregation (Wagemans et al. 2012).

[32] A promising theory of consciousness holds that conscious representations and states are characterized by the integration of information, or more precisely, on the formation of complexes of integrated information (Tononi 2004, 2008, 2012). That integrated information characterizes consciousness is, however, mainly derived from a set of axioms and introspective or intuitive thought experiments, most of which have already been discussed in the previous text or footnotes (Tononi 2012). What this review of experimental findings however shows is that the "integration of information" comes in many guises, not all of which are equally strongly related to consciousness. A somewhat more precise definition of "integrated information" may be guided by these experimental findings.

[33] The figure is 4 degrees of visual angle wide. Neurons in human V1 with receptive fields at that distance are about 20 mm apart, given a cortical magnification factor of 0.2 degrees per millimetre at 2.0 degrees eccentricity (Duncan & Boynton 2003).

textual Gestalt effects typically manifest themselves at long latency.

Intuitively, seeing an illusion like the Kanizsa triangle, or the contextual shifts in brightness or colour perception discussed above, also seems to depend on "long range" interactions: information travels over large distances in the visual field. But distance travelled over the visual field does not always equal distance travelled in the brain. These phenomena may depend on fairly hardwired and feedforward mechanisms, and their neural correlates typically have relatively short temporal latencies (Von der Heydt et al. 1984). Seemingly, these phenomena tap into mechanisms that have high ecological relevance to the visual system, and are hence solved in a few processing steps, using dedicated feedforward mechanisms. The same holds for all categorization responses in the brain, regardless of their apparent complexity: the progression from low-level to high-level feature detection (including categorization of faces or other complex stimuli) proceeds in a feedforward "sweep" that lasts 100 ms or less (Lamme & Roelfsema 2000).

What emerges is the nagging feeling that consciousness has nothing to do with the seeming complexity or "high-levelness" of a visual function. Whether a visual function depends on consciousness may simply be related to the amount of space that has to be travelled in the brain, how many processing steps have to be taken in between, and hence how much time it takes to complete. This converges onto a thesis that we may call:

> The STERP-property of phenomenal representations $=_{\mathrm{Df}}$ conscious representations depend on the spatio-temporally extended neural processing mediated by recurrent interactions.

What that extent is remains to be specified, but has been studied directly by Faivre & Koch (2014), who measured the effects of stimuli made invisible using CFS on the perception of subsequent visible stimuli. Both for apparent motion and for biological motion walkers, it was found that unconscious motion integration only occurred for relatively short (100 ms) and not for longer (400, 800, 1200ms) temporal intervals. Meng et al. (2007) observed that neural signals representing the spatial filling-in of a grating over a gap in the visual field depended on conscious experience of the grating.[34] This suggests that for visual information to literally "bridge a distance" across the visual field, consciousness is required.

The importance of the spatial and temporal extent of neural processing in consciousness also emerges from an entirely different field: that of disorders of consciousness. It is generally believed that there is a gradual decrease of consciousness from the healthy awake state towards minimally conscious, vegetative state and coma. These states also show a gradual decrease in the extent of neural interactions, in both space (Casali et al. 2013) and time (Bekinschtein et al. 2009). Particularly striking is the finding that the presence or absence of consciousness (in this case: the difference between minimally conscious and vegetative state patients) could be classified by simply looking at the amount of "shared symbolic information" in the EEG[35] at various distances in the brain. Shared symbolic information at distances of 10 cm and beyond signalled the presence of consciousness, and moreover was indicative of the prognosis of vegetative state patients (whether they would eventually awaken or not). Strikingly, this measure hardly depended on the location of the interactions (King et al. 2013). In other words, whenever and wherever neurons share information at distances of 10 cm or more, there is consciousness.[36]

Both distance and time are continuous. Arguing that consciousness is related to the temporal or spatial extent of neural processing therefore almost automatically seems to imply that the transition from unconscious to con-

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[34] It did not depend on attending the grating, however, which is of relevance to the discussion on the relation between attention and consciousness. See below (Lamme 2003, 2004, 2006, 2010a, 2010b).

[35] At each electrode, EEG signals were first transformed into symbolic shapes (e.g., up-down-up) for various temporal intervals. Then it was determined to what extent these EEG "symbols" covaried between electrode pairs of various distances, after the exclusion of covariance that was caused by simple volume conduction.

[36] Which made me wonder whether any piece of cortex of 10 cm or larger that is held on life support in a petri-dish might have consciousness.

scious processing is gradual rather than discrete. This is not necessarily so, however. Recurrent processing is mediated by highly nonlinear interactions, and in such interactions, rather discrete phase transitions are possible (Steyn-Ross et al. 1999; Del Cul et al. 2007; Hwang et al. 2012). It could thus very well be that there is a discrete transition from a phase where information integration is rather limited to a phase that is characterized by extensive information integration, and that this transition depends on the temporal or spatial extent of recurrent interactions.[37]

Whether the transition from unconscious to conscious processing is discrete or continuous has been argued on different grounds, such as on the distribution of behavioral responses (“seen” versus “not seen”) in relation to manipulations of stimulus variables (Sergent & Dehaene 2004; Overgaard et al. 2006). In signal detection theory, the strength of perceptual information is considered to be continuous, while the decision criterion imposes a discrete boundary between what is reported as “seen” or “not seen”. In its classic form, however, signal detection theory is agnostic about whether consciousness is pre- or post-decisional. Recently, many attempts have been made to incorporate consciousness into the framework of signal detection theory, and in many of these models consciousness is considered post- rather than pre-decisional (Maniscalco & Lau 2012; King & Dehaene 2014)—thus the boundary between the conscious and unconscious is taken to be discrete. Based on neurophysiological findings in the monkey visual cortex, a signal-detection model was devised in which consciousness was considered pre-decisional. In this model, the distribution of sensory information was considered bi-modal, reflecting either a conscious or an unconscious state. The model could explain both the behavioral and neurophysiological findings in the monkey visual cortex, obtained using a variety of stimulus strengths and decision criteria (Supèr et al. 2001). Note that also in this pre-decisional model the conscious–unconscious divide is discrete (or at least bi-modal), rather than gradual.

10 The function of conscious vision

Could it be that Gestalt grouping and figure-ground segregation (of textured images) only happen to go along with consciousness because they take more time; because they require more elaborate computations, not provided by the many dedicated feedforward pathways and modules of the brain? Normally, vision proceeds in a fast and feedforward fashion, where dedicated neurons detect features and categories. Using its hardwired connections, the visual system can swiftly detect the most relevant objects: food, mates, or dangerous animals. Some objects are more difficult to discern, and require prior knowledge or the computation of neighbourhood relations between image elements: food behind a leaf, a sweet versus a sour apple. That takes slightly more—but not too much more—time, because many of the required interactions are hardwired as well. They are hardwired because the visual system has been exposed to these “visual problems” very often, either during evolution or during visual experience. Then there are visual problems that are even more difficult: a camouflaged animal in a crowded forest (figure 7), only visible via subtle differences in overall texture or motion. In this case, all visual resources and mechanisms have to come to the rescue. Only by combining the input from many neurons in a versatile way can the visual “solution” be found. That may be the function of consciousness in the visual domain: to combine the otherwise unconscious modules and mechanisms in a flexible way so as to solve otherwise unresolvable visual problems leading to a second thesis that we may call:

> The SUPER-property of phenomenal representations $=_{\mathrm{Df}}$ neural representations require consciousness and invoke phenomenality as soon as what needs to be represented can no longer be represented by a single dedicated module or mechanism, yet

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[37] It could even be that the mere fact that information exchange extends over a particular time and space is critical for that exchange to be accompanied by a conscious sensation. When the same amount of information would be exchanged much slower — as in plants — or much faster — as in a supercomputer — or over a smaller or larger space (as in a microchip or over the internet) no conscious sensation ensues.

requires the interaction of these modules so that a super-positioned representation emerges.

From the point of view of consciousness, a hierarchy of visual functions can then be made. This starts with largely unconscious feature detection and object categorization. These features start to influence each other, and are no longer treated independently, so that categories form that are about the relations between image items (base groupings, short range incremental grouping). With this, there is a transition from the physical properties of the visual input as they are presented to the sensor array to the meaning[38] of these properties (e.g., wavelength to colour). During these operations, features and categories are matched with our knowledge and expectations of the world, embedded in the anatomical organization of the visual cortex, aiding in the transformation from visual input towards meaning (inference). Finally, all this information is combined into an organized percept. The longer these operations take, the more distance has to be travelled in the brain, and the more conscious these operations become.[39]

If nothing interferes, the visual system will always strive towards optimally integrating the available information, so that the richest interpretation of all available information is achieved, and all features have been detected, all inferences have been made, all image elements are combined and all potential ambiguities have been resolved. If this process is cut short, for example by masking or a TMS pulse (Pascual-Leone & Walsh 2001; Silvanto et al. 2005), there is no integrated end-result. And seemingly there is no conscious sensation either. Regardless of this, many features have still been detected, many inferences have been made, and the brain can use this information to achieve its goals. Behaviour may be influenced, or set into motion (Dehaene et al. 1998). Priming will occur, as well as all sorts of unconscious cognition (Van Gaal & Lamme 2012). Without consciousness, and without maximal integration, the visual system is far from helpless. It can do less, but it can still do a lot.

From this perspective, the function of consciousness in vision is just to enable that last push. That is, to resolve the visual issues that cannot be dealt with otherwise.[40] And with that, visual functions grow more complex, and evolve from their basic form into more sophisticated versions. A good example comes—once again—from the processing of faces. The core property of face-selective neurons is to respond in a category-selective manner: they distinguish between faces and other objects. They do so from the very first action-potentials that are fired. At that moment, however, category specificity is still very basic, in the sense that all types of faces evoke a similar response (Rolls 1992). At a later moment in time, however, responses typically become more and more specific. In the monkey visual cortex, face cells distinguish between different viewpoints and different emotional expressions of faces with a delay of about 50 milliseconds relative to the categorical face/non-face response (Sugase et al. 1999). View invariant identity representations arise even later, with a delay of about 200 ms (Freiwald & Tsao 2010). At these delays, the face-selective neurons will have established recurrent interactions with lower (and higher) level neurons across the brain, allowing for these more sophisticated classifications to be expressed in the response.

We may thus conclude that face recognition "as we know it"—i.e., not just categorizing face versus non-face, but seeing that face, knowing what it looks like, who it is, and what emo-

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[38] Note that "meaning" in this context refers to the meaning information has to the organism, shaped by and in accordance with its evolutionary history and ontogenesis (like colour has the "meaning" of the edibility of fruit). It does not refer to "meaning" in any linguistic sense.

[39] That may explain why two seemingly similar phenomena like the brightness and colour shifts of figure 2, and the arrival at colour constancy in figure 3 are depend on consciousness in different ways. Colour constancy requires the computation of the full distribution of wavelengths over the entire image, which takes more time than the computations required to compute brightness of adjacent patches.

[40] Maybe that is the reason why the transition from unconscious to conscious processing also marks the transition between veridical and inferred representations (e.g., from wavelength to colour). Dedicated modules can do their thing in isolation, and therefore have no need to compromise towards a non-veridical representation of the outside world. When modules interact, the necessity may arise to compromise veridical representations to achieve global coherence into the combined super-positioned representation that cannot be represented otherwise.

tion it carries—is a visual function tightly linked to conscious rather than unconscious vision. The main reason for this lies in the fact that in conscious recognition we go beyond simple categorization, and move towards a function where the integration of all possible information about that face (its viewpoint, colour, identity, emotional expression, etc.) is required.

This may raise the question of how we then become conscious of an extremely simple stimulus, such as an oriented black line on a completely white background. With such a simple stimulus, there seems to be no need for any elaborate binding, incremental grouping, or inference. Neurons in the primary visual cortex can detect the line and its orientation within a few action potentials. There seems to be no need to call in the functions that are enabled by conscious processing. So why is it, then, that we still see the black line on the white background?

First, it should be noted that the notion of "simple" stimuli is more complex than one would expect. For example, it was shown that subjects can rapidly detect animals or vehicles in complex natural scenes, even when their attention is simultaneously focused on another task. Discriminating large T's from L's, or bisected colour disks from their mirror images was impossible under the same dual task paradigm. Apparently, seemingly simple letter or disk stimuli require more attentive processing than seemingly complex natural scenes (Li et al. 2002), suggesting that they take longer and more elaborate processing. In blindsight, subjects can discriminate lines of different orientations, suggesting that conscious processing is not required for these simple stimuli. However, discrimination performance—although above chance—is typically worse than for consciously-seen line segments, suggesting that something is "missing" from the neural representations formed in blindsight compared to those in conscious vision.

So what might the more elaborate processing steps that lift the unconscious representation of a black line towards a conscious representation of that line be? First, it is known that neurons in many visual areas beyond V1 respond to orientated line segments. At each level, receptive fields, and hence spatial frequency preferences, differ. This means that (the orientation of) the line segment is represented at many different spatial scales across the visual cortex. Only the integration of these differently-scaled representations, via recurrent interactions, yields a precise and conscious representation. The same holds for other properties of the "simple" line segment, such as its colour, its depth, and its relation to the background.[41] Indeed, oriented lines are fairly easy to mask (in fact easier than faces), indicating that their conscious percept depends on more elaborate processing steps than expected for such a simple stimulus.

11 The impact of conscious vision on the brain

If a particular visual problem has to be dealt with often, the brain will start to build connections so that the problem can be resolved more rapidly. Visual problems that require long and elaborate processing will eventually be resolved in milliseconds. By building new and dedicated connections, elaborate processing steps may be simplified into a fast and short set of interactions. Conscious processing will turn into unconscious processing, because conscious processing has triggered perceptual learning that in turn evokes synaptic changes that create new "dedicated modules" that can do the job unconsciously. This leads to a third thesis:[42]

> The LEARN-property of phenomenal representations $=_{\mathrm{Df}}$ neural representations that require consciousness and invoke phenomenality, at the same time evoke synaptic plasticity mechanisms and learning,

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[41] Even something as simple as a white background will give the black line another visual "meaning" than a yellow background, a green background, or a textured background. The same point has been formulated by Giulio Tononi (2004, 2008, 2012): a conscious representation is conscious because it differentiates from the endless other potential representations that could have been. In this case: the oriented black line on the white background is one of the endless possible configurations of lines on backgrounds, and only by integrating the information of line and background is it known which of these configurations is actually present.

[42] Similar ideas exist in the context of motor learning: a task that first requires extensive conscious practice will gradually become more and more automatic, up to the point where it can be executed fully unconsciously.

in an attempt to make these representations less dependent on consciousness and invoking less phenomenality.

Indeed, there are several arguments for linking consciousness to perceptual learning. Plasticity in the visual cortex comes in many temporal and spatial scales. There are fast- and short-range adaptations or recalibrations, expressed in altered stimulus-response dependencies (e.g., contrast normalization). But receptive fields may also change in size or feature selectivity when exposed to repeated stimulation. Receptive fields literally grow or shift position when their surrounds are stimulated but the receptive field is not (Gilbert & Wiesel 1992). Prolonged depletion of input leads to the induction of new connectivity via fast axonal sprouting of horizontal connections (Yamahachi et al. 2009). Horizontal connections in particular play an important role in both immediate and longer term plasticity of the visual cortex (Gilbert et al. 1996). The repeated execution of Gestalt grouping via the same connections may therefore induce learning (Gilbert et al. 2001), as, for example, is observed in the learning of texture segregation (Karni & Sagi 1991) or in the gradual improvement of contour integration during childhood development (Kovács et al. 1999). In addition, perceptual learning induces a reorganization of the areas involved in encoding the learned object—a process that is mediated by feedback connections (Sigman & Gilbert 2000; Sigman et al. 2005). It seems that the neural machinery that mediates Gestalt grouping and segregation is also the machinery that mediates perceptual learning.

Furthermore, feedback and horizontal connections have been linked to the molecular mechanisms of neural plasticity. A key component in neural plasticity is the NMDA receptor pathway, and in the monkey, NMDA receptor blocking using APV reduces contextual figure–ground modulation (Self et al. 2012). Similarly, in humans, figure–ground segregation is impaired using Ketamine, an anaesthetic which selectively blocks the NMDA receptor at low doses (Meuwese et al. 2013). Also, it was found that Ketamine at sub-anaesthetic doses interferes with the leaning of Mooney figures. Mooney figures are high-contrast versions of images that are hard to recognize when you don't know what the image is about. Once you have seen its original natural contrast version, however, the Mooney image is readily recognizable. It was found that the neural representation of Mooney images starts to resemble that of their natural versions once they are learned. Ketamine disrupts this rapid learning process, but only in V1, and not in higher visual areas, indicating that feedback from higher areas to V1 is selectively disrupted by Ketamine (Van Loon et al. submitted).

In sum, there are strong indications that link conscious visual processing and its neural machinery—horizontal and feedback connection—are linked to perceptual learning and the molecular mechanisms involved. This may open up a path to a more molecular understanding of consciousness. In addition, it provides us with a clear idea about the function of consciousness: that of building a new repertoire of visual functions, so that eventually conscious processing is no longer necessary.

It must be noted however, that the link between consciousness and learning is controversial. Many instances of "unconscious" perceptual learning exist (e.g., Gutnisky et al. 2009; Seitz et al. 2009; Seitz & Watanabe 2003; Schwiedrzik et al. 2011). An important issue here, however, is whether these are cases of learning without conscious experience of the stimuli that induce the learning, or whether they are instances of learning without cognitive access or attention to these stimuli (see Meuwese et al. 2013). A further clarification of the role of consciousness in learning is required.

12 The dolphins of consciousness research

I have examined the defining characteristics of conscious versus unconscious vision. Incremental grouping and segregation according to Gestalt laws seems to be a defining characteristic of conscious vision. Other visual phenomena and functions, like interference or inference, are less strongly linked. Feature detection and higher-level categorization clearly do not mark the transition from unconscious to conscious vision. From a neural perspective, it can be argued that conscious processing is linked to those operations that require spatially and temporally extended processing, where neurons engage in incremental interactions involving many steps. These processes are selectively dependent on horizontal and feedback connections. Moreover, these interactions induce learning, as they operate along highly plastic neural pathways, and use the molecular machinery that is directly involved in neural plasticity.

We can now start using these defining characteristics to answer more difficult questions. Is there consciousness in the right half-brain of a split brain patient (Sperry 1984)? Is there consciousness without attention (Koch & Tsuchiya 2012)? Is there consciousness in neglect or extinction (Lamme 2003)? Is it appropriate to talk about inattentional "blindness", where people do not remember having seen something while their attention was engaged elsewhere? What exactly happens during change blindness (Simons & Rensink 2005)? Is there consciousness in animals (Edelman & Seth 2009), or in a vegetative state (Owen et al. 2006)? These are the "dolphins" of consciousness research, situations that are hard to position in the current taxonomy of conscious versus unconscious, because much controversy exists about the presence or absence of conscious experience in those conditions. With this, I hope to have given some usable arguments that can settle such controversies. My claim would simply be that whenever we see the defining properties of conscious vision that have been laid out here (i.e., incremental Gestalt grouping and segregation), there is conscious vision, regardless of whether there is conscious access or report (e.g., Scholte et al. 2006). More in general, the more fruitful stance towards consciousness would be to let all the available evidence converge into general theses, such as those derived here, and then take these as the defining characteristics of conscious processing and consciousness, regardless of whether they fit our introspective intuition of what consciousness is or should be. Defining consciousness as the process that builds on spatio-temporally extended neural processing (STERP property), that enables the building of super-positioned representations that individual modules cannot provide (SUPER property), and that evokes synaptic plasticity and learning (LEARN property) yields clear defining characteristics. These characteristics go a great length towards elucidating important features of phenomenality (its integrated nature, Gestalt properties), towards explaining the nature of conscious experience (perceptual organization, interference, inference), and are hinting towards a potential function of consciousness (learning) and its molecular basis. What I consider irrelevant characteristics (such the ability to report about an experience, see Lamme 2010a, 2010b) generally do no such explaining. It is better to build a taxonomy of conscious versus unconscious processing on defining characteristics than on irrelevant ones. That has helped a lot in positioning dolphins in the taxonomy of species. It will also help a lot in positioning the wild amalgam of phenomena that the field of consciousness research has produced so far. And it will enable us to give consciousness its proper ontological status. But I have already contributed to that discussion extensively elsewhere (Lamme 2003, 2004, 2006, 2010a, 2010b), so I will lay that to rest here.

At the crack of dawn, something magical happens. Night turns into day, life springs, vibrations fill the air. We know, it is just the earth rotating. But a very fundamental transition it remains. Unconscious or conscious processing, it's all neurons doing their job, firing action potentials, exchanging chemicals, transferring information. But somehow, suddenly, they "turn on the light". You see. You have a conscious sensation of that dawn. Isn't it beautiful? You should take a picture of it.

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