A new low: Reassessing (and revising) the local recurrency theory of consciousness

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Abstract

Local Recurrency Theory (LR) holds that recurrent loops of neural activity localized to the visual cortex are necessary and sufficient for visual consciousness (if certain background conditions obtain). LR's popularity has recently waned in favor of theories holding that higher-level types of processing are necessary for consciousness (e.g., the Global Neuronal Workspace Theory and Higher-order Theory). This has been in part because of empirical evidence thought to disconfirm LR. However, these competing theories now face challenges of their own, often coming in the form of evidence showing that higher-level brain areas (i.e., in the prefrontal cortex) are probably not essential for consciousness. Given growing challenges to LR's competitors, it would be timely to re-assess the prospects for LR. This article carries out such an investigation, first laying out the theory precisely, then going on to survey the evidence presented against it. What will be found is that none of the evidence necessarily undermines LR, but instead just fosters its theoretical enrichment. The overall conclusion: LR remains among our most promising neuroscientific theories of visual consciousness.

0. Introduction

Notable progress has been made toward the goal of having a neuroscientific account of visual consciousness, and the many theories offered in recent decades are now arguably whittled down to a few competitors. Three of these would be *Local Recurrency Theory*, which holds that consciousness occurs when the right kind of feedback loops obtain between visual brain areas (Lamme 2003, 2006, 2010), *Global Neuronal Workspace Theory*, which holds that visual consciousness occurs when information is widely distributed among the brain's subsystems via a frontoparietal network (Dehaene et al. 2006, 2014), and *Higher-order Theory*, which holds that

visual consciousness occurs when the prefrontal cortex re-represents visual states (Lau & Rosenthal 2011; Lau & Brown 2019).¹

Recent history has seen Local Recurrency Theory eclipsed by Global Neuronal Workspace Theory and Higher-order Theory, in part because of evidence taken to conflict with Local Recurrency Theory (hereafter, LR) (Driver & Vuilleumier 2001; Marois et al. 2004; Del Cul et al. 2007). However, Global Neuronal Workspace Theory (GNW) and Higher-order Theory (HO) now face serious challenges of their own. One problem stems from their commitment to the prefrontal cortex (PFC) being crucial for consciousness (e.g., Lau & Rosenthal 2011; Mashour et al. 2020), since recent years have seen the emergence of strong evidence and arguments against this idea (Boly et al. 2017; Raccah et al. 2021), especially from cases where prefrontal lesions fail to lead to the kinds of conscious deficit that would be expected if the PFC was essential for consciousness (Pollen 2007; Kozuch 2014, 2021; but see Michel 2022). Given the growing challenges that GNW and HO face, it would be timely to re-assess the prospects for LR. This article carries out such an investigation, doing so by examining the evidence that is often taken to disconfirm LR. What is found is that all of this evidence either does not conflict with LR, or requires only minor amendments to the theory. In fact, instead of the evidence in question undermining LR, it is catalytic to its theoretical enrichment. The overall conclusion of this article will be that LR remains a promising theory, one to be considered a leading contender for being the correct neuroscientific theory of visual consciousness—especially given mounting problems for GNW and HO.

While this article's focus is LR, the arguments given here are ultimately in service of a larger debate, this being between *Local* and *Broad* neuroscientific theories of visual consciousness (Michel & Doerig 2021). According to *Local* theories, of which LR is one, activity in just visual areas can be sufficient for visual consciousness (Zeki & Bartels 1999; Zeki 2003; Lamme 2006, 2010, 2015; Block 2007);² according to *Broad* theories, of which GNW and HO are both examples, areas outside of the visual cortex are also required (e.g., Dehaene & Changeux 2011; Lau & Rosenthal 2011; Brown et al. 2019). The debate over Local versus Broad theories is probably more significant than the one over whether specifically LR, GNW, or HO is

¹ Another contemporarily popular theory is Tononi's Integrated Information Theory (IIT) (Tononi 2004; Oizumi et al. 2014), which explains consciousness by using a mathematical framework that shows how certain kinds of physical systems could instantiate the kinds of property that we associate with conscious experience (e.g., the way that it contains structured representations, and seems irreducible to its parts). Space limitations prevent us from considering theories other than GNW and HO, which collectively act as a much neater foil to LR than does IIT.

² It is probably the case that, in addition to visual cortex activation, some kind of subcortical background conditions must obtain, such as there being certain kinds of activity in the brain stem (see, e.g., Alkire & Miller 2005; for discussion, see Block 2009).

true, not least of all because many Broad theories (including GNW and HO) take the prefrontal cortex to play a constitutive role in visual consciousness (Lau & Rosenthal 2011; Michel & Morales 2020). Among the things at stake in the debate concerning the PFC (see also Michel & Doerig 2021) is that its outcome probably has important repercussions for animal consciousness (and therefore animal welfare), given that few animals have prefrontal areas anatomically or functionally resembling our own (Kaas 2013). For these reasons, this article's larger goal is not really to see whether LR itself can be preserved, but rather whether some suitably modified version of it could be considered a plausible theory of visual consciousness, since this would mean that we had a plausible Local Theory of consciousness. Note that this is why it won't matter, when we get to article's end, whether the modified Local Theory at which we have arrived *counts* as a version of LR or not.

Here is the article's layout: Section 1 reviews some of the evidence for LR, and presents a working formulation of LR. Then each of the next four sections examines one line of evidence offered against LR: Section 2 considers neuroimaging evidence taken by some commentators (e.g., Dehaene et al. 2006, 2014) to present instances of recurrency without consciousness; Section 3 considers lesion evidence that has been taken by some commentators (e.g., Lau & Brown 2019) to present instances of visual consciousness without V1 involvement, something that would seem to be in conflict with LR, as it's classically conceived; Section 4 considers other lesion evidence seeming to show that, under rare circumstances, visual consciousness actually can arise without V1 involvement; Section 5 discusses psychophysical experiments that have been taken by some commentators (Michel & Doerig 2021) to present instances of recurrency without visual consciousness; Section 6 presents an updated formulation of LR, one taking into account the data reviewed in the article. What emerges from our investigation is a version of LR that is empirically adequate and theoretically enriched, a neuroscientific theory of visual consciousness among our most promising.

1. Local Recurrency Theory, motivated and formulated

In this section's first part, we examine LR and the positive case for it, surveying some of the theory's confirming evidence. In the second part, we investigate the issue of how LR should be understood, and give a precise formulation of the theory. I note that this article does not intend to present an *exhaustive* case for LR (more support for the theory can be found in (Lamme 2004, 2006, 2010, 2015; Van Gaal & Lamme 2012)), the main goal instead being just to present enough supporting evidence to make LR look like a promising neuroscientific theory of consciousness—one worth defending against the objections considered later in the article.

1.1 The case for LR

According to LR (Lamme 2004, 2010, 2015; van Gall & Lamme 2012), visual consciousness is realized by a certain kind of dynamic interaction between areas in the visual cortex,³ something known as *recurrent processing*. Recurrent processing (RP) is distinguished from the feedforward sweep (FFS), the initial wave of information about a stimulus that travels from the back to the front of the cortex, first up a hierarchy of visual areas, then on to non-visual brain areas (Lamme & Roelfsema 2000). The FFS reaches the highest levels of the visual cortical hierarchy by about 100ms after stimulus presentation, and the PFC by about 150ms. Shortly after the FFS reaches any given brain area, RP begins, and the firing of individual neurons start to reflect input from sources not just below them in the hierarchy, but also from areas above, along with horizontal influences from the same level. The rapid, iterated exchange of information enabled by RP allows a neuron's response to gradually evolve so that it reflects not just those properties falling in its receptive field (e.g., what texture is located there), but also more global properties (whether the texture belongs to an object or its background) (Lamme & Roelfsema 2000). Many visual properties are detected during the FFS, not just lower-level properties such as orientation, shape, or color, but also higher-level properties such as whether something is a face or not. It seems, however, that RP is required for more complex and global kinds of visual processing, such as when individually represented properties (e.g., orangeness, roundness) are transformed into coherent percepts (seeing the orangeness and roundness as belonging to a tangerine) (Lamme 2010). In the thesis of LR, it is this dynamic and recursive kind of neural activity, i.e., recurrent processing, that is hypothesized to be capable of generating visual consciousness, even when localized entirely to the visual cortex (given certain background conditions).4

One motivation for adopting LR as a theory of visual consciousness comes from its ability to explain a wide range of neuroscientific data concerning conscious versus unconscious processing (for reviews and arguments, see Lamme 2004, 2006, 2010; van Gaal & Lamme 2012). In the flagship study for LR (Pascual-Leone & Walsh 2001; see also Silvanto et al. 2005), transcranial magnetic stimulation (TMS) was used to depress activity in V1 just after motion-sensitive area V5.⁵ Typically, stimulating V5 causes a moving phosphene (a small streak of

³ For the purposes of this article we take the *visual cortex* to consist of early visual areas (e.g., V1 and V2), along with areas in the ventral processing stream (e.g., V4, LO, IT), and area V5. Areas in the dorsal stream (those in the posterior parietal lobe) have not played a role yet in debates concerning LR, and space limits prevent our considering them here.

⁴ For information about the background conditions, see fn. 2. From here, I stop explicitly adding this qualification each time I discuss the thesis of LR, but LR should still be understood as including it.

⁵ V1 (AKA the primary visual cortex) is the area where most visual information first enters the cortex, and V5 is a mid-level visual brain area specializing in motion-processing.

light). However, on trials where TMS was used to suppress activity in V1 just after stimulating V5 (~25ms later), the subject failed to experience the phosphene. LR explains this intriguing result as occurring because suppressing activity in V1 interrupted the incipient recurrent loop caused by V5 stimulation (Lamme 2006, 2010). In another study supporting LR (Amassian et al. 1989), suppressing occipital cortex activity with TMS at 80-100ms SOA (stimulus onset asynchrony)⁶ was shown to prevent conscious perception. Since this is likely to be too late to affect the FFS (Lamme & Roelfsema 2000), LR explains the lack of consciousness as resulting from the TMS interrupting the potential RP (see also Amassian et al. 1993). Numerous other experiments also showing long latency TMS to prevent conscious perception provide support for LR for the same reason (Masur et al. 1993; Jolij & Lamme 2005; Silvanto et al. 2005; Koivisto et al. 2011, 2017; Railo & Koivisto 2012; Hurme et al. 2019).

Other empirical support for LR comes from backward visual masking (Enns & Lollo 2000), the experimental phenomenon in which consciousness of a first stimulus is prevented by presenting another "masking" stimulus shortly thereafter (50-100ms SOA) (see also Lamme et al. 2002; Fahrenfort et al. 2007; Boehler et al. 2008). LR explains this as occurring because the masking stimulus disrupts and supplants the incipient recurrent loop caused by the first stimulus, something suggested by the timing at which the mask needs to be presented for suppression to occur. In one particularly interesting masking study (Ro et al. 2003), carefully timed TMS (100-140ms post-*mask* presentation) applied to early visual areas⁷ prevented the stimulus from being masked, presumably doing so by interrupting the RP of the mask, but not of the target. It should be noted that some commentators explain visual masking without appealing to recurrent loops, using a feedforward model that hypothesizes the masking to occur because of lateral inhibitory mechanisms (Herzog et al. 2003; Macknik & Martinez-Conde 2007), with one line of evidence for this view coming from experiments that have been taken to indicate that, when TMS is used in the pro-LR studies discussed above, it might be used early enough to interfere with the feedforward signal (Center et al. 2019). We set aside the issue of whether these criticisms are apt.

There are, in any case, other lines of evidence supporting LR: There is a study showing that the absence or presence of RP between the inferotemporal cortex (IT) and earlier visual areas predicted whether or not a face stimulus would be consciously experienced (Fahrenfort et

⁶ Stimulus Onset Asynchrony: the amount of time passed since the target stimulus was presented.

⁷ The experimenters took the TMS suppression to predominantly affect V1, but also possibly V2 and V3 (V2 and V3 sit just above V1 in the processing hierarchy, but below mid-level areas such as V5).

al. 2012).⁸ LR can also be taken to be supported by the phenomenon of blindsight (Weiskrantz 1996), since LR does a good job of explaining the particular patterns of deficit that blindsighters suffer from: Their inability to consciously experience visual stimuli can be explained by their V1 damage, since this would prevent RP from arising, while their ability to make accurate reports about stimuli can be explained by mid-level brain areas (e.g., V5) still receiving information via connections with subcortical areas (Stoerig & Cowey 1995, 1997; Pollen 1999). Also supporting LR would be the fact that, when a person becomes blind, it is typically only when their blindness was caused by something other than V1 damage that they continue to have visual experiences (in the form of phosphenes or hallucinations), since this suggests that those subjects that lack any kind of visual experience do so because V1 damage prevents RP from forming (Bender et al. 1968; Kölmel 1984). Finally, some commentators argue for LR by pointing out how RP enables some kinds of processing that are defining of conscious vision, things such as feature integration (e.g., seeing properties as bound to objects) and perceptual learning (e.g., learning to recognize what is depicted in an ambiguous image) (Lamme 2010, 2015).

It seems, then, that there is copious evidence confirming LR. Something to note here is that some of this evidence might not *uniquely* support LR, since certain versions of GNW (e.g., Mashour et al. 2020) might be construed as also taking RP in visual areas to be necessary for visual consciousness. In such a version of GNW, the content of visual consciousness is constituted, not by activity in the frontoparietal network (i.e., not in the areas composing the global workspace), but rather by RP in visual areas; instead, the frontoparietal network just acts as a router for the to-be conscious content (for discussion: Michel 2022). We put this point aside, however, since this section's goal is not to show that LR is uniquely favored by the evidence, but rather just that it is empirically well-motivated. Now we turn to the issue of how LR should be more precisely understood.

1.2 Formulating LR

Despite LR having enjoyed popularity (Lamme & Roelfsema 2000; e.g., Block 2005, 2007; Lamme 2010; Van Gaal & Lamme 2012), certain aspects of the theory are yet to be stated formally. Nonetheless, if one surveys the literature concerning LR theory, one finds a few reoccurring commitments, and these can be used to assemble a working formulation of LR. To introduce it, we again consider the 2001 Pascual-Leone and Walsh experiment.

⁸ Fahrenfort et al. inferred whether RP was occurring by looking for potential markers of it, such as the synchronized firing of neurons (as measured by EEG) or increased functional connectivity (as measured by fMRI) between IT and early visual areas.

This study showed that using TMS to suppress V1 shortly after stimulating V5 (~25ms after) prevented the conscious perception of a phosphene; this has been taken to show that what constitutes conscious motion perception might be a recurrent loop between V5 and V1 (Lamme 2004; Block 2005). This suggests a way of interpreting LR according to which what constitutes conscious visual content of each type (e.g., color, motion, etc.) will be a recurrent loop between V1 and whatever area specializes in processing the type of content in question (cf. Stoerig 2001). So, just as conscious motion perception is constituted by RP between V1 and V5, conscious shape perception will be constituted by RP between V1 and shape-sensitive area LO (lateral occipital cortex), and conscious color perception by RP between V1 and V4, and so on. This brings us to our first working formulation of LR:

For all lower-level visual content C, C is conscious if and only if it is represented in recurrent loops between V1 and a higher-level brain area

Note that the formulation can be taken to make two claims: The first is the *Processing Claim*, which says that RP is essential for consciousness; the second is the *Locational Claim*, which says each instance of RP that results in consciousness will involve, as its substrate, V1 and a higher-level brain area.⁹

The above statement of the theory is on the right track, but needs three amendments. Each are discussed in their own subsection.

1.2.1 LR as a theory of lower-level visual consciousness

Consider the issue of which brain areas LR would hypothesize to underly higher-level types of visual experiences, for example, experiencing an object as being of a certain type (e.g., experiencing something as *being a dog*) (Kriegel 2007; cf. Siegel & Byrne 2017). It is natural to assume that such an experience would involve the area in the brain that carries out object recognition, this being the high-level visual area the inferotemporal cortex (IT) (Van Essen & Anderson 1995).¹⁰ But when considering the issue of which brain area(s) IT will engage in RP with, there are multiple options: It could be that the loop is with V1; alternatively it could be with one or more mid-level brain areas (V4, V5, LO, etc.). Intuitively, the latter is more

⁹ It should be noted that, though LR locates consciousness at a low level of processing (early and midlevels), there are theories on the offer that hypothesize that activation of V1 alone can be sufficient for visual consciousness (i.e., no other cortical brain areas are necessary) (Linton 2021).

¹⁰ It is controversial as to whether object recognition ever actually *has* phenomenal character (see the discussion of "high-level" phenomenology" in (Kriegel 2007)).

attractive, given that the function of object recognition will rely on the kinds of information that mid-level brain areas process, things like an object's color, motion, shape, etc.¹¹

We sidestep this issue, amending LR so that it concerns just what I will call *lower-level* types of conscious visual content, properties such as brightness, hue, shape, and motion (to name a few). So, our goal in this article will be to see whether LR is an adequate theory of how lower-level visual content arises.

Note also now that the brain areas that specialize in processing each of these types of content are located at what could be considered the mid-level of visual processing; this being the case, we will below modify the Locational Claim of LR so that it says that the involvement of specifically *mid-level brain areas* is necessary for (lower-level) visual consciousness to arise.

1.2.2 V2's role in consciousness

A second amendment concerns LR's requirement that V1 be a participant in all instances of visual consciousness. This comes from a consideration of the possibility that other early cortical visual areas also play some kind of role (Stoerig 2001; Block 2019). Some prominent candidates would be V2, V3, and V3A. Here, we lack space for discussing what role each of these brain areas might play in consciousness, so we instead focus on just V2, an area that is—in any case—probably the best candidate of the three for playing such a role.¹² In regards to how V2 might be involved in consciousness, there are three main possibilities, each of which we'll look at now.

A first option here is that it is not RP between V1 and a mid-level brain area that is necessary and sufficient for consciousness, but rather RP between V2 and a mid-level brain area. A second option would be that neither V1 nor V2 is necessarily involved in any instance of visual consciousness, but rather either V1 *or* V2 (Block 2019).¹³ Both of these options look unlikely to be true, given that the data reviewed above (in 1.1) strongly suggested that V1 is necessary for at least many visual experiences.¹⁴ Given this, we set these two options aside.

In a third option, it is held that RP that obtains just between V1 and a mid-level brain area is not sufficient for visual consciousness, since V2 must also be involved in the RP (Pollen 1999; Stoerig 2001). Some reason to think this comes from how V1 is more sparsely connected to

¹¹ Additionally, V1 lacks direct connections with IT (Felleman & Van Essen 1991).

¹² In the case of V3, damage here does not seem to cause deficits of visual consciousness (Pollen 1999), and in the case of V3A, it is part of the dorsal visual processing stream, something for which we have some reason to think that it operates without consciousness (Kozuch 2015, 2022).

¹³ In Block's 2019 article, he seems to be considering the possibility of both options.

¹⁴ I am grateful to an anonymous referee at this journal for having stressed this last point.

extrastriate¹⁵ brain areas than is V2 (Felleman & Van Essen 1991; Van Essen & Anderson 1995), since this means that RP that included V2—perhaps as an intermediary between V1 and a midlevel brain area—might be more robust than RP that did not include V2. Also supporting V2's necessity are studies showing that late suppression of V2 by TMS (44-104ms SOA) prevents conscious experience of a stimulus (Salminen-Vaparanta et al. 2012), since this plausibly occurs because the TMS interrupted a recurrent loop involving V2 (but see Merigan & Maunsell et al. 1993). Other data supporting the necessity of V2 come from studies showing that V2 lesions cause scotomas in one's visual field (Horton & Hoyt 1991; McFadzean & Hadley 1997). On the other hand, ablations in primates that carefully target V2, but leave intact connections from V1 to higher visual areas, prevent perception of more complex properties (e.g., viewer-independent shape) but not simpler ones (brightness) (Merigan & Maunsell 1993). So perhaps the safest hypothesis here is the one saying that V2 is only necessary for the perception of more complex visual properties.

Overall, it looks like there is notable evidence in favor of V2 being necessary for visual consciousness, at least in the case of more complex properties. To reflect this possibility, we will below modify the Locational Claim of LR, so that it no longer says that it is "V1" that is necessary for consciousness, but rather "early visual areas."

1.2.3 What kind of RP?

A last amendment to be made to LR concerns its Processing Claim, the idea that RP is sufficient for consciousness (when between early- and mid-level visual areas). Given currently limited knowledge, it would be appropriate to have LR formulated in such a way that it says that it is not necessarily *just any kind* of recurrent activity that is sufficient for visual experience, but rather the *right kind*. I will explain.

Given that LR (like all current neuroscientific theories of consciousness) is still a relatively new theory, we should think about it as a *general form* of a neuroscientific theory, one to be filled out in response to theoretical developments and emerging data. The idea here is that there might be extra conditions that need to obtain before content can become conscious, i.e., conditions going beyond the content merely being represented in RP. It could be the case, for example, that not all kinds of RP are sufficient for visual consciousness, but rather just certain sub-types; or it could be that RP must be sustained for some relatively long time before a stimulus becomes conscious, at least in the case of certain more complex stimuli. These extra conditions are something that will be discovered in the course of research; indeed, we discover

¹⁵ "Extrastriate" means outside of the primary visual cortex (V1), the name coming from V1's striped appearance.

some below. In any case, it is because of observations like these that we will formulate LR with an "in the right way" clause, one to be filled as we go.

1.3 Second formulation of LR

Now we add the three amendments to LR, the ones saying (1) that LR concerns *lower-level* experience, (2) that LR leaves open the possibility that V2 is also necessary for consciousness, and (3) LR holds that it is only the *right kind* of RP that is sufficient for visual consciousness. Here it the updated formulation:

For all lower-level visual content C, C is conscious if and only if it is represented (in the right way) in recurrent loops between early and mid-level visual areas

What we have seen in this section is that LR is a fairly well-defined theory with an impressive body of empirical evidence confirming it. This makes LR a promising neuroscientific theory of visual consciousness. Of course, LR is not the only such theory receiving empirical confirmation, this also being true of Higher-Order and Global Neuronal Workspace Theories (for reviews: Lau & Rosenthal 2011; Dehaene et al. 2014; Lau & Brown 2019; Mashour 2020). Given this, what becomes particularly important when deciding between these theories is how well each fares with attempts to empirically disconfirm it. As noted above, there is strong disconfirming evidence in the case of HO and GNW, some of it taking the form of data showing the PFC to be not essential for consciousness. This makes the question of whether there is any evidence disconfirming LR all the more interesting, and so this is the issue that the rest of the article investigates. Below, we examine neuroimaging and psychophysical evidence (Sects. 2 and 5, respectively) thought to show that RP can occur in visual areas without consciousness arising, and brain lesion evidence (Sects. 3 and 4) thought to show that visual consciousness can arise without V1 involvement.

2: Purported cases of recurrency without consciousness

Often, critics of LR (e.g., Dehaene et al. 2006, 2014; Michel 2022) offer neuroimaging evidence against LR. This usually takes the form of studies where a visual stimulus causes significant activation (in some form) of visual areas without its being consciously perceived. Such evidence threatens LR if the enhanced activation can be taken to suggest that the unconscious stimulus had been represented in recurrent loops, something that would contradict the idea that RP is sufficient

for consciousness. What we see in this section is that each study fails to disconfirm LR.¹⁶ This will often be because, in these studies, trials where the stimulus is not consciously perceived are accompanied by significantly decreased visual area activity, something suggesting that the stimulus failed to be represented in recurrent loops. We look at the evidence.

In one of the earlier studies thought to support a role for the PFC in consciousness (Dehaene et al. 2001), a visual mask was employed,¹⁷ and fMRI was used to compare levels of brain activation shown on trials where the word was unmasked, and therefore consciously perceived (call these "conscious trials"), to ones where it was masked ("unconscious trials"). These results have been taken to confirm GNW (Dehaene & Changeux 2011) because frontoparietal areas (those taken to constitute the global workspace) showed significantly decreased activation on unconscious trials (only 5% of what was seen in the case of unmasked words). At the same time, these results cannot be said to disconfirm LR, since a significant difference in activation between conscious and unconscious trials was also seen in visual areas, with activation reaching only 19% in extrastriate visual cortex, and 9% in the fusiform cortex. This decreased activation can plausibly be taken to suggest that the target stimulus was not represented in RP, in which case this study does not disconfirm LR.

A similar difference in visual area activation levels can be found in each of the other fMRI experiments to which LR's critics have appealed. In a study by Haynes and colleagues (2005), the experimenters presented subjects with a metacontrast mask while using fMRI to record from several levels of visual processing. Conscious versus unconscious trials were again found to cause not just increased frontoparietal activity, but also significantly increased visual area activity at every level of processing (e.g., V1, V5, and the fusiform gyrus). In a study by (Zou et al. 2016), binocular rivalry was induced using a horizonal grating fed to one eye, and a vertical grating to the other, causing the subjects' conscious perception to oscillate between the two. Notably, it was found that a suppressed grating would still cause an increased BOLD signal¹⁸ in parts of the visual cortex (e.g., V1 through V4), but this activation was greatly reduced, only about 10% of what was seen in response to the non-suppressed grating. Then there is a study employing hemispatial neglect (Vuilleumier et al. 2001) that is taken to count against LR since it showed that faces presented in the subject's neglected field caused activation of their

¹⁶ Definition: We can consider datum D to *disconfirm* theory T if one of T's predictions is not-D. So, what I will be arguing below is that most of the data fails to fall outside the predictions of LR.

¹⁷ In contrast to the *backward* masking discussed in 1.1 (where the mask is presented just *after* the target), this was *forward* masking: A noisy stimulus was presented just *before* the target (a word), and this caused the subject to not consciously experience it.

¹⁸ BOLD = blood oxygen level dependent, i.e., a measure of how blood is flowing to that part of the brain.

contralateral fusiform face area (FFA); however, this FFA activation is significantly reduced relative to what is seen when the face is presented in their non-neglected visual field.¹⁹And, in the case of each of the other fMRI studies to which LR's critics have appealed, there is a similar (and significant) reduction in visual area activity on unconscious trials, where this reduction can plausibly be taken to indicate that the stimulus failed to be represented in RP (Carmel et al. 2006; Jiang et al. 2007; Fahrenfort et al. 2012; Wyart et al. 2012; Van Vugt et al. 2018).

Other studies that critics of LR have appealed to, ones employing other neuroimaging techniques, appear susceptible to the same objection. For example, in an attentional blink experiment by Sergent and colleagues (2005), EEG was used to track neural activity in both conscious and unconscious trials. A significant difference between the two was not found until 180ms SOA, at which point there would be a distinctive kind of increase in frontoparietal activity, the P3b component (something that the GNW theorist has sometimes taken to be the neural signature of consciousness (Dehaene & Changeux 2011)).²⁰ However, something else found only on conscious trials after 180ms was a significant increase in visual area activity. Since this increased activity can be interpreted as reflecting the formation of RP at this later stage (i.e., after 180ms), these results are not in conflict with LR.²¹ A different study used *intracranial* EEG to record from areas in the occipital, fusiform, and frontal cortex (Gaillard et al. 2009), finding that conscious trials were accompanied by more widespread and higher levels of activation (starting 150ms after stimulus presentation), with this not occurring just in prefrontal areas, but also in higher- and lower-level visual areas. Similar points can be made about each of the other EEG studies enlisted as evidence against LR (Marois et al. 2004; Del Cul et al. 2007; Pitts et al. 2012).

Other neuroimaging studies mentioned as being evidence against LR also fail to conflict with it. In a study by Sahraie et al. (1997), fMRI was used to measure neural activity in a subject with blindsight (GY) while motion stimuli were presented to either his sighted or blind hemifield. Notably, conscious trials brought increased dlPFC activity, this being true whether the

¹⁹ Additional reason to think that this study does not count against LR comes from compelling arguments that neglect is merely a disorder of attention, and not of consciousness (Lamme 2006; Block 2007; Jacob & de Vignemont 2010; Kozuch 2014, 2015, 2022).

²⁰ This idea has recently fallen into disfavor due to some experiments showing the P3b component to correlate with consciousness only when the consciously experienced stimuli are *task-relevant* (Cohen et al. 2020; for discussion, see Michel 2022).

²¹ They might, however, be in conflict with Local Theories that hold that 150ms of processing should be sufficient for visual consciousness, an example here perhaps being Zeki's "micro-consciousnesses" theory (2003).

consciously perceived stimulus had been presented to GY's sighted or blind hemifield.²² A similar increase in activity, however, was also found in area V2, something suggesting that RP (between V5 and V2) might have been formed on conscious trials.²³ Next we consider some studies involving motion-induced blindness,²⁴ ones showing that when the target stimulus disappeared from consciousness, this was accompanied by an *increase* in activity in those parts of visual cortex where the stimulus was represented (Schölvinck & Rees 2010; Davidson et al. 2020). However, this very local increase in activation probably results from neural competition created by the visually ambiguous stimulus (Scholvinck et al. 2010), in which case the increased BOLD response probably comes from (a) the inhibitory spiking that causes the target stimulus to disappear from consciousness, and/or (b) the visual system actively filling-in, in those parts of the visual field where the stimulus was presented, the color of the stimulus background.

It seems, then, that all of the neuroimaging studies thought to contradict LR arguably fail to do so. In many cases, this is because there is a lower level of activation shown by visual areas on unconscious as opposed to conscious trials, something suggesting that recurrent loops were never formed.

3: Purported cases of conscious experience without V1

As it is construed here, LR hypothesizes lower-level visual consciousness to occur only when there is RP between early- and mid-level brain areas. Given this, some evidence used against LR consists of cases in which V1 is damaged (or absent) and yet visual consciousness remains. For example, Lau and Brown (2019) argue against LR by appealing to certain rare cases of Charles Bonnet syndrome, ones in which subjects with V1 damage experience hallucinations. Before discussing this evidence, we first look at the issue of when we should consider V1 lesion evidence to count against LR.

A first issue here concerns what LR must predict in cases of V1 damage. What is most important to note here is that LR need not predict that *any* case of V1 damage will *completely eliminate* visual consciousness (like it is in cases of complete blindness), but rather just that visual consciousness will be degraded *to the same degree* that V1's functionality is (with elimination of visual consciousness occurring only when functionality is entirely lost). Another

²² Despite GY's being clinically blind in his right hemifield, there are certain kinds of stimulus that he sometimes consciously experiences, one example here being quickly moving stimuli. For more analysis of his case, see discussions of GY in the next section.

²³ For more analysis of this case, and why it's friendly to LR, see discussions of GY in the next section.

²⁴ A paradigm in which a circularly moving background causes a stationary target stimulus to become invisible to the subject.

thing to consider here is that the amount by which visual consciousness is degraded might be lessened by *neuroplasticity*, the process by which the brain can sometimes partially recover some of the functionality that was lost because of a lesion (Grafman 2000; Grafman et al. 2010). The idea that neuroplasticity can sometimes mitigate the effects of brain damage should always be followed up with the caveat that such mitigations are rarely complete, and often only provide a modest recovery of function (Frost 2003; Grafman 2000; Grafman et al. 2010; for discussion, see Kozuch 2023), full recovery being something that typically occurs only in very young patients (e.g., Vargha-Khadem et al. 1997). It is important to note this since, in debates concerning neuroscientific theories of consciousness, the powers of neuroplasticity are sometimes implied to be much stronger than this (Lau & Rosenthal 2011; Morales & Lau 2020). But let us return to the main point: The fact that neuroplasticity sometimes brings about modest recovery from brain damage (or more pronounced recovery with very young patients) can be enlisted by LR to explain why a brain-damaged subject's visual consciousness appears to be *somewhat less* degraded than might expect, given the severity of the V1 damage. Let us keep these points in mind while examining the V1 lesion data.

As mentioned above, Lau and Brown (2019) have tried to argue against LR by appealing to Charles Bonnet Syndrome (CBS), a disorder in which deafferentation of the visual cortex (or parts of it) causes benign but persistent visual hallucinations.²⁵ It should be noted that Lau and Brown seem to be swimming upstream here, against what might be the dominant view, which is that such hallucinations occur only if V1 is preserved (Bender et al. 1968; Kölmel 1985; Anderson & Rizzo 1994; Pollen 1999). This view is based upon numerous studies showing that hallucinations occur only if V1 is preserved, and that they will be isolated to parts of the visual field from which V1 still processes information (Gloning et al. 1967). The next thing important to note is that the studies to which Lau and Brown appeal do not contradict this view, since in each case damage to V1 is incomplete (it is often unilateral), leaving open the possibility that undamaged portions of V1 still participate in recurrent loops, ones that underly the patients' hallucinations (Block 2019). Additionally, in the first study (Duggal & Pierri 2002), the patient's vision partially and gradually returned following her infarction, suggesting that the damaged hemisphere had recovered some function and/or the undamaged hemisphere had taken on some of that function; and in the second study (Ashwin & Tsaloumas 2007), the damage is not only unilateral, but also appears incomplete, since the patient was still able to consciously perceive items appearing in central parts of his contralesional hemifield.

²⁵ The hallucinations can be exceptionally creepy (disembodied faces with staring eyes) or fanciful (a procession of tiny costumed people in hats).

Other cases of V1 damage with residual conscious vision are explained in similar fashion: In (Henriksson et al. 2007), a hemiblind 61 year-old patient with unilateral V1 damage was rehabilitated using flicker stimulation, and eventually started to have primitive experiences of form and brightness in his blindfield; however, it is clear that this is because the undamaged hemisphere had taken on some of the function of the damaged side, as fMRI revealed that consciously perceived stimuli in either visual field activated visual areas in just the undamaged hemisphere. And a patient who natally acquired severe bilateral V1 damage presented with only somewhat impaired vision at the age of five, but this is probably the result of strengthened connections between extrastriate visual areas and the lateral geniculate nucleus,²⁶ something detected by using diffusion tensor imaging (Amicuzi et al. 2006). Other cases of bilateral V1 lesions can be explained by the incompleteness of the damage and/or youth of the subjects when the damage occurred (Giaschi et al. 2003; Bova et al. 2008; Muckli et al. 2009).²⁷

In summary, in the case of the evidence involving V1 damage with residual visual consciousness just reviewed, nothing falls outside of the predictions of LR. But that does not mean that all of the evidence concerning V1 lesions are breezily explained by LR, this being the matter to which we turn next.

4: Actual cases of visual consciousness without V1

Although LR explains most instances where there is still visual consciousness with damaged V1 by appealing to the incompleteness of the damage or the possibility of neuroplasticity, there are three cases not as susceptible to this kind of explanation, ones perhaps qualifying as instances of visual consciousness without functioning V1.

The first two types of cases come from instances in which there is unilateral damage to V1, something that results in blindness for half of the visual field ("hemianopia"), where this blindness occurs in the hemifield opposite lesion location (i.e., it is "contralesional") (Silvanto & Rees 2011; for reviews: Mazzi et al. 2019). The first type of case consists of studies where subjects are able to perceive the entirety of a centrally presented object, including the half appearing in their blindfield. For example, in (Marcel 1998), it was found that a conscious afterimage could be produced for the half of a Gestalt figure that was presented in the blindfield, as long as the other half was simultaneously presented in the sighted field (Warrington 1962,

²⁶ A part of the thalamus, the subcortical sensory area just below V1 in the processing hierarchy.

²⁷ Due to space limits, this article focuses on addressing empirical objections to LR that have been raised by LR's opponents that have not yet been addressed. Nonetheless, it should be mentioned that arguments exist in the literature for the idea that V1 is not necessary for dreaming (Rees et al. 2002) or visual imagery (Kleiser et al. 2001), but reasons for thinking that these arguments do not undercut V1's role in consciousness (along with reviews of the relevant data) can be found in (Stoerig 2001) and (Ganis 2013).

1965; for other examples, see McCarthy & Warrington 1986). In the second type of case, bilateral stimulation of extrastriate brain areas is shown to be able to produce experiences in the blindfield. An example of this would be a study done with blindsighter GY (Silvanto et al. 2007, see also 2008), in which it was shown that TMS targeting just the half of V5 located on the same side of the V1 lesion (i.e., the "ipsilesional" side) caused no visual experience in the blind hemifield, but that a motion phosphene is produced if the stimulation was carried out bilaterally (similar studies include Bender & Kahn 1949; Torjussen 1976). The third type of case is Riddoch syndrome (Riddoch 1917), cases in which subjects that are blind from V1 damage are still able to sometimes experience motion, especially high-speed stimuli (Riddoch 1917; Weiskrantz et al. 1995; Zeki & Ffytche 1998). This is an ability that blindsighters also often display, under the proper experimental conditions (Foley 2015).²⁸ The motion experience such subjects have appears to be very impoverished, in that they describe it as an experience of something that is moving, but which lacks shape and color (Zeki & Ffytche 1998).

The cases just examined are not all easily explained by incomplete damage or neuroplasticity,²⁹ since the blindness that these subjects experience seems to imply that the relevant parts of V1 (i.e., those parts contralateral to the blindness) have little or no remaining functionality. As well, the spontaneous and selective way in which these experiences arise makes it less likely that they are made possible by neuroplasticity, since this is usually a gradual process (but see Voytek et al. 2010). And so these studies appear to be in conflict with the idea that V1 is necessarily involved in any RP that brings about visual consciousness. At the same time, we saw a large amount of data above showing that disrupting V1 activity prevents consciousness of the stimulus, suggesting the necessity of V1. How are these data reconciled?

I believe that these data are best explained by V1 being necessary for visual consciousness under most circumstances, except in those rare instances where other forces are available to help engender RP. That is to say, these data might show that there are infrequent instances in which visual consciousness arises without V1, but they do not show that visual consciousness arises without RP (cf. Silvanto 2015). Let us look at why.

Consider how in the first two types of studies (i.e., those involving hemianopia and unilateral V1 damage), the stimulus bringing about the blindfield afterimage does not work unless presented bilaterally, suggesting that the representation of the figure in contralesional cortex is somehow helping to *empower* the representation of the figure in the ipsilesional cortex,

²⁸ Whether the stimulus is consciously perceived will be determined by factors such as its luminance, or the speed of onset and offset.

²⁹ Although, as Mazzi (2019) points out, in many cases of Riddoch syndrome, it is was not confirmed that V1 was completely destroyed (Teuber et al. 1960), in which case residual V1 might make the motion experiences possible.

supplementing it to the point where the representation becomes conscious. Something reinforcing this interpretation would be the fact that such a technique works best when a Gestalt figure is used as a stimulus (Marcel 1998; Mazzi 2019), since we would guess that the kind of holistic perception that they engender would plausibly increase the degree to which the two hemispheres operated synergistically. Consider also that TMS to V5 of a blindsighter produces no experience of motion if such stimulation is only ipsilesional (Cowey & Walsh 2000), but does so if the stimulation is bilateral (Silvanto et al. 2007). These studies suggest that contralesional V5 is somehow contributing to the robustness of the representation in ipsilesional V5, where this might be supplemented by the extensive connections that V5 has with the LGN of the thalamus (Bridge et al. 2008; Ajina et al. 2015). This interpretation receives further support from the stimulation having to occur in a precise order for experience of motion to arise—ipsilesional before contralesional but not vice versa—and from the dense transcallosal connections that human V5 has (Riedel et al. 2004), ones which have been, in the case of GY, further enriched through neuroplasticity (Bridge et al. 2008). As well, V2 appears to be sometimes playing a role in generating the conscious experience, since a study with GY showed an increase in V2 activity each time GY experienced a moving stimulus in his blindfield (Sahraie et al. 1997). Finally, the necessity of the stimulation being bilateral is also seen in studies where color adaptation is used in combination with TMS to bring about color experiences in the blindfield (Silvanto et al. 2008).

The data just reviewed suggests that conscious perception in a blindfield is somehow brought about by synergistic processing between the two sides of a brain area. This synergistic processing, furthermore, invites being interpreted as having been accomplished through RP; however, in this case, the loops are not between a mid-level brain area and V1, but rather between (a) the ipsilesional side of a mid-level brain area and (b) the LGN, V2, and/or the contralesional side of the same brain area.

Moving on to Riddoch syndrome, the subjects' ability to still consciously perceive motion can be explained by appealing to many of the considerations discussed just above, in that many of V5's exceptional characteristics can help explain how it could generate RP in absence of V1. First, V5 has robust and direct connections to two subcortical structures, the LGN (of the thalamus) and the pulvinar (Ajina et al. 2015; Bridge 2008), something that has been thought to mean that V5 will start to rely more heavily on input from these structures once V1 is damaged (Ajina et al. 2015); this, in turn, means that neuroplasticity is likely to make such connections stronger over time. As well, V5 possesses dense transcallosal connections (Riedel 2004), ones whose robustness has been demonstrated by studies showing these connections to be particularly active when viewing motion stimuli requiring interhemispheric processing (Genç et al. 2011). These connections, of course, are likely to be strengthened through neuroplasticity after V1's loss, just as they were in the case of GY. Overall, a number of V5's features make it a good candidate for producing RP without that aid of V1, especially in the case of the faint, phenomenologically impoverished motion experiences that subjects with Riddoch syndrome have, since such experiences probably require only a weaker form of RP to arise.

At this point, we have been led to a modified LR, one with a weaker Locational Claim. According to this version, what is essential for visual consciousness is not participation by V1 per se, but rather the formation of the right type of recurrent loops. In turn, the tight correlations between V1 activity and consciousness seen in the empirical data surveyed above can be explained by hypothesizing V1 (and V1 alone) to be *reliably* effective at engendering the loops. The effectiveness with which V1 can do this could potentially be attributed to something unique about V1's physiology, connectivity, and/or position in the visual processing hierarchy (one possibility here being the rich connections it has with numerous extrastriate visual areas (Felleman & Van Essen 1991; Polack & Contreras 2012)). Discovering exactly what makes V1 unique in this way is a goal of future research.

In any case, the overall idea here would be that V1 is *typically* necessary for forming the RP that constitutes (low-level) visual consciousness, but that these loops can sometimes form in cases where other means exist for engendering them (cf. Stoerig 2001). So far, we have seen that this might occur when TMS is used to boost brain activity, or when especially strong stimuli (e.g., Gestalt figures) are presented. The idea that V1 is only typically necessary will appear later in the updated and modified formulation of LR given in this article's last section. At that point, there is also further discussion as to what consequences this has for LR as a theory.

This "Modified LR" leads to predictions. The first one builds off of the Pascual-Leone and Walsh experiment (2001) discussed above. In that study, unilateral TMS suppression of V1 performed about 25ms after ipsilateral V5 stimulation prevented the V5 stimulation from causing a moving phosphene. Modified LR suggests that, if one used this paradigm, but were to also stimulate contralateral V5 just after stimulating ipsilateral V5, this might allow contralateral V5 to stand in for V1 as a partner in RP, thereby reinstating the phosphene experience (in the same way that I hypothesized it to be doing in the hemianopia studies examined above (e.g., Silvanto et al. 2007)). The next prediction is based on a paradigm used by Jolij and Lamme (2005), one in which TMS to V1 delivered at 110ms SOA was shown to prevent conscious perception of a face. Consider, now, an experiment that is similar, but which uses multiple types of stimulus (including Gestalt stimuli), and which suppresses V1 unilaterally rather than bilaterally. Here, Modified LR suggests that V1 suppression is less likely to prevent conscious perception of the stimulus if the stimulus is Gestalt and presented centrally (like it was in (Marcel 1998)), than it would be if it is either (a) non-Gestalt or (b) presented unilaterally in the hemifield contralateral to V1 suppression. One more prediction: We saw above how Modified LR partially explains the residual ability of V1-damaged subjects to experience motion (both in the case of blindsight and Riddoch syndrome), doing so by noting the extensive subcortical and transcallosal connections that LR possesses, something that might engender RP in V1's absence. On the basis of this, we can predict that the less connectivity that a visual area possesses, the more susceptible its ability to contribute to consciousness should be to disruption by lesions or TMS to the relevant parts of V1.

Now we move on to consider one more line of evidence presented against LR.

5: Psychophysical experiments purported to show recurrency without consciousness

Recently, Michel and Doerig raised a challenge to LR using *postdictive effects*, i.e., cases where multiple, sequentially presented stimuli are integrated into a single conscious stimulus (2021). An example of this would be how a red disc presented just before a green disc causes perception of a singular yellow disc (Efron 1967). Michel and Doerig take these to be cases in which a stimulus is represented in recurrent loops for an extended period without becoming conscious, a counterexample to LR. We start by looking at the experiments, then move on to discuss why they don't count against LR.

5.1 The postdictive experiments and LR

The experiments to which Michel and Doerig appeal involve figures known as "verniers," sets of two vertical, parallel lines that are offset horizontally by a small amount. In one experiment (Scharnowski et al. 2009), two verniers with opposite offsets are presented one directly after the other, each for 30ms (Fig. 1). The subject perceives a singular vernier, one matching one of the verniers in the direction of its offset (depending on which vernier "dominates"), though its offset is reduced relative to the dominant vernier. Scharnowski et al. applied TMS to the occipital cortex at varying times from stimulus onset, finding early applications (45ms-95ms SOA) caused second vernier dominance, and late applications (95-370ms SOA) caused first vernier dominance. Michel and Doerig (hereafter, "M&D") take the fact that which vernier dominates can be affected by TMS for up to 370ms SOA to mean that "the two verniers are represented independently" for an extended time, this happening prior to when the two representations are used to form a "single fused representation" (p. 4). M&D take this to mean that the stimulus "is stably represented [in recurrent loops] but not consciously perceived" (p. 6), a counterexample to



Fig. 1: Rapid serial presentation of two verniers can result in conscious perception of a single fused vernier, one with an offset matching that of one of the two verniers, but which is reduced. (From Scharnowski et al. 2009.)

the idea that recurrent activity in the visual cortex is sufficient for consciousness. Let us call this first experiment the *TMS Vernier Study*.

In a second experiment (Drissi-Daoudi 2019), a Sequential Metacontrast (SQM) paradigm was employed (see Otto et al., 2006). In SQM, a number of vertical bars are presented sequentially in neighboring locations, creating the illusion of vertical bars moving laterally from central vision toward the periphery (see Fig. 2). In the experiment to be considered, it was found that inserting a vernier in the first frame caused the subject to perceive the moving object as being the vernier rather than any of the subsequently presented lines. Important to present purposes is a further finding, which was that the perception of the vernier could be altered by presenting another vernier, even at relatively long SOAs. For example, if a vernier with an offset *opposite* from the first is substituted for one of subsequently presented lines, and this is done within 450ms SOA, the verniers cancel out, and a moving line is perceived. Here, M&D claim that the fact that "observers report seeing only the integrated percept and cannot report on the individual verniers...suggests that the first vernier is represented without being perceived for up to 450ms" (p. 5). Since this is probably long enough for the stimulus to start to be processed in recurrent loops, M&D consider this to be another counterexample to LR. Call this the *Moving Vernier Study*.

Let us evaluate this objection. As seen above, M&D seem to take there to be stable, fully formed representations of the stimuli that fail to be consciously perceived. For example, in the



Fig. 2: Postdictive effects in a Sequential Metacontrast (SQM) paradigm. Rapid presentation of lines and/or verniers causes the perception of two diverging motion streams. In Set 1, using a vernier in the first frame causes a perception of a moving vernier. In Set 2, putting a second contradictory vernier amidst the subsequently presented lines causes the verniers to cancel one another out, and a moving line is perceived instead.

first study discussed just above, M&D believe that representations of the two verniers coexist for an extended period of time, from when the stimuli are presented until the conscious perception is formed (at least 370ms later). However, this interpretation of this experiment (see also Herzog et al. 2020), which we can call "Stable Representations" (or "Stable," for short), is not the only explanation available. Indeed, the authors of the TMS-vernier study themselves (Scharnowski et al.) reject this explanation in favor of one according to which there are no stable or fully formed vernier representations until stimuli integration is complete. According to this "Unstable Information" explanation ("Unstable," for short), quick presentation of two conflicting verniers creates a situation in which incipient representations of the stimuli start to compete with one another, the result being mutual suppression. This mutual suppression keeps the information being processed about each of the verniers in too unstable of a form for it to organize into a fullblown representational state; instead, this information only acts as input to the representation eventually experienced. Note now that, if Unstable is true, then LR can be reconciled with the postdictive data: LR need not be committed to the idea that, in any instance where information about a visual stimulus is processed for an extended period, this results in its being consciously perceived; instead, a more principled version of LR is one according to which such information becomes conscious only when it has organized into something resembling a stable representation. Below, I explain why this version of LR should be preferred, and what consequences it has for their theory. For now, I just note that the postdictive data does not threaten this form of LR, not unless there is reason to think that the unconsciously processed vernier information is in the form of stable representations, i.e., that Stable is true. And, as I show now, there is reason to doubt that it is.

Consider how, in the TMS Vernier Study, when the two verniers of incompatible offsets are presented in quick succession in the same location (Fig. 1), this (metaphorically) creates a puzzle for the visual system: How could two differently shaped objects appear in the same place, more or less simultaneously? And in the case of the Moving Vernier Study, the stimuli are similarly contradictory: The first two stimulus frames were (1) a vernier presented centrally for 30ms followed by (2) two vertical lines presented for 30ms, one just left of central vision, the other just right (Fig. 2). This brings about multiple ambiguities: Is it the case that each of the three presented figures are distinct objects, or is it that the first object is identical to one of the other two, but has moved? If it *is* identical to one of the two objects, which one? And, finally, does this hypothesized self-same object possess an offset, and if so, how large?

Taking into account the above considerations, it seems unlikely that the information being processed unconsciously about the postdictive stimuli is in the form of stable representations. Instead, the information more likely remains in a volatile state that is an unruly admixture of information from both figures, one which could tip toward becoming a representation of one figure or the other (or something in between), but has not yet done so. At the neural level, the conflicting stimuli probably bring about *lateral inhibition* (Scharnowski et al. 2009), with the quick presentation of contradictory figures causing the groups of neurons responding to the first and second figure to go into a cycle of mutual suppression. It is interesting to note, furthermore, that we can estimate how long the information being processed stays in a "suspended" state by indexing it to the latency at which an intervention still affects conscious perception. For example, in the TMS Vernier Study, the fact that TMS can affect vernier dominance for up to 370ms SOA indicates that it took the visual system at least that long to coalesce into a stable interpretation of the stimuli (e.g., it took that long for it to settle on what offset the vernier had), and this provides some reason to think that information about the relevant stimuli stayed in an unstable form for the same amount of time. And in the Moving Vernier Study, the fact that presenting a conflicting vernier within a 450ms window could alter the subject's experience can be taken to show that, at 450ms SOA, the visual system had not yet built a stable representation of the first vernier (or the subsequent lines).³⁰ It is worth noting that the long latency at which the vernier perception could be affected in the Moving Vernier Study should probably not be considered all that surprising, given that the stimulus is being interpreted as moving, and motion processing is something that must be spread out in time (unlike, for example, when stationary stimuli are analyzed, something that can potentially be based on a visual "snapshot") (Herzog et al. 2020).

Overall, there is a strong case for the idea that unconscious information about the postdictive stimuli is not in the form of stable representations. Now recall what I said above, which is that LR need not be committed to the idea that anytime information about a stimulus is processed for an extended period, it becomes conscious. Instead, LR should hold that this happens only when stimuli are *stably represented*. And, since it looks unlikely that the unconscious information about the postdictive stimuli is in the form of stable representations, the postdictive studies do not count against this form of LR. In the next section, we further develop this response to the postdictive studies.

5.2 Requirements for consciousness: Stability and actionability

We just saw that there is a satisfactory response to the postdictive effects-based argument against LR: Intuitively, the information about the postdictive stimuli isn't in the form of stable representations, and LR can be understood as requiring stable representation for consciousness. Now we make the response more detailed, and provide motivation for making this addition to LR.

We start by saying what is meant by "stable" and "representation," starting with the latter first. Defining "representation" is not simple, given the long-standing debates concerning its nature (see, e.g., Artiga & Sebastián 2020). To work around this, I will instead just *stipulate* that representation (*for the purposes of LR*) be understood as being something that requires *actionability*. For a definition of actionability, we can understand some informational state S to be actionable if and only if it can be used, by other parts of the cognitive system to which it belongs, as an indicator that something is p resent in the environment, e.g., if it can be used as

³⁰ To put the point in a more precise way, the visual system seems to have been *on its way* to creating a stable representation of the first vernier, but had not yet done so by the time at which the second vernier was introduced; that it was on its way to doing so can be gleaned from the fact that, in trials where the second vernier is not presented, subjects report having seen a moving vernier whose offset matches that of the first vernier.

an indication that a circle appeared in central vision (cf. Dretske 1988, Ch. 3).³¹ In regards to "stable," this can be understood as the ability of an informational state to maintain its actionability even when perturbed or intervened upon: An informational state satisfying this criterion will be unlikely to lose its actionability when, for example, the stimulus is overlapped by another object, or when suppressing TMS is given to the brain area where the stimulus is represented. Note now that these two conditions indeed do not seem to be satisfied by the unconsciously processed information about the postdictive stimuli: That the information probably lacks stability comes from the way in which late interventions (i.e., the TMS or additional stimuli) can affect what stimulus is consciously perceived, and that it probably lacks actionability comes from the way in which the information remains in a disorganized and fluctuating state, something that would make it difficult for other parts of the cognitive system to use the information as an indicator that some item in the environment.³² In sum, we now have a more precise proposal concerning the addition to be made to LR, which is to say that a stimulus can be perceived consciously only if it is *stably* and *actionably* represented. While we lack space for an investigation into what the neural bases of stability and actionability might be, some plausible candidates would be synchronic activity, increased functional connectivity, and/or the convergence of individual neurons on an attractor state (Varela et al. 2001; Fahrenfort et al. 2012; Herzog et al. 2016): These seem to be plausible candidates since each seems like a potentially effective neural means for preventing an informational state from losing its integrity (stability), and for enabling its usage as a symbol of something in the environment (actionability).

Now we discuss why these additions to LR are well-motivated: Remember that I above opted to *stipulate* how "representation" should be understood for purposes of LR. It would be a mistake, however, to think that this stipulated definition of "representation" has no close connection with what representation actually *is*. This is because information remaining in too disorganized of a form to be used as a symbol of something in the environment (i.e., information that lacks *actionability*) arguably does not rise to the level of actually *being* a representation.

³¹ Of course, representations can be of things other than those in the environment (e.g., representations can represent other mental states), but I artificially delimit the definition here so as to make it more easily understood.

³² Stability and actionability seem to be closely related insofar as it is plausibly the case that whether information is stable or not might be what largely determines whether it is actionable or not. For example, it is plausible that information that is able to withstand perturbation can do so because it is in a wellorganized and resonant state; similarly, it is also plausible that it is because it is in a well-organized and resonant state that is suitable for use as a symbol of something in the environment. It might even turn out that stability is necessary and sufficient for actionability, in which case there might be no need to independently appeal to each in a formulation of LR; but this is not issue that this article will attempt to further investigate.

Given this, there is another way to understand the response to the postdictive data given above, which is to understand it as arguing (1) that the unconscious postdictive stimuli information stays in too disorganized of a form to be representational, and (2) that a necessary condition on information becoming conscious is that it be representational. Note now that, if we construe LR as saying that visual consciousness cannot arise in the absence of bona fide representation, this means that the claim that LR is adopting here does not go beyond a claim having the virtue of already being widely accepted, this just being the idea that all visual experiences are representational: While some philosophers hold that there is *more* to conscious experiences than their representational content (Block 1996; Papineau 2021), there are no philosophers (to my knowledge) that deny that each instance of visual consciousness *has* representational content (Jackson 2003). In sum, since the idea that stability and actionability are necessary conditions for consciousness is tantamount to making *representation* necessary for consciousness, and since this latter claim is widely accepted, it seems that the addition of these to LR as necessary conditions as compulsory for any plausible theory of consciousness.

This addition to the theory provides new ways to confirm or disconfirm LR. Consider a case in which information about a stimulus has been processed for an extended period without becoming conscious, which means that enough time has passed that RP might have arisen. In such a case, it seems that the absence or presence of the neural markers of stability and actionability could be used to confirm or disconfirm LR, with their absence acting as confirmation, and their presence as disconfirmation. For example, if we had reason to think that (as suggested above) synchronic activity is a neural marker of stability/actionability, then the absence of synchronic activity during extended unconscious processing confirms LR, and its presence disconfirms LR.

Now we move on to the task of presenting and discussing the final formulation of LR that this article will provide.

6: Local recurrency theory, reformulated

This section reviews what happened in the article, and provides a formulation of LR updated to account for data examined above. A good way to start is by re-stating our original, working formulation of LR from Section 1.3:

For all lower-level visual content C, C is conscious if and only if it is represented (in the right way) in recurrent loops between early and mid-level visual areas

In the article, we saw two lines of evidence offered against LR that turn out to not threaten it: In Section 2, the neuroimaging studies offered as evidence for recurrency without consciousness was not in conflict with LR, usually because a lack of conscious perception was always accompanied by significantly reduced activity in visual areas (suggesting that recurrent loops were never formed). In Section 3, the lesion data that was purported to show visual consciousness to occur without V1 could all be explained by appealing to neuroplasticity or incomplete V1 damage, which meant that V1, or some brain area standing in for it, was available to participate in whatever recurrent loops constituted the conscious experiences.

However, two other lines of evidence that we examined did require modifications to LR. In Section 4, there were studies in which conscious experiences without V1 could be induced using TMS or an especially strong stimulus (a Gestalt figure). The way that LR explains this is by saying that, while participation of V1 is usually necessary for forming the RP that constitutes visual consciousness, RP can form without V1 if there is some other force available (e.g., TMS, high stimulus strength, extra neural pathways), one that helps engender recurrent loops. Assuming these data are as they seem, they require dropping the Locational Claim from LR's formulation, i.e., the idea that all lower-level visual consciousness requires involvement of *both* early and mid-level visual areas. We do this below.

At the same time, the idea that lower-level visual consciousness cannot, in typical circumstances, arise without V1 is still significant: The goals of a complete neuroscience of consciousness will of course include discovering which neural structures frequently realize our visual experiences, and the data reviewed above seem to support the idea that it is early- and mid-level brain areas that do so. Additionally, the idea that RP between early- and mid-level brain areas is *sufficient* for consciousness (if certain background conditions obtain) puts LR in conflict with other currently ascendent theories of consciousness, e.g., Global Neuronal Workspace Theory, since GNW holds that content must reach frontoparietal areas before becoming conscious. For these reasons, our formulation of LR below will include modified Locational Claims, presented as two auxiliary theses, one saying that visual consciousness is typically realized in RP between early- and mid-level brain areas, and another saying that such activity is sufficient for visual consciousness.

The other line of evidence that required modifying LR was in Section 5, where we saw cases in which information about stimuli (verniers and lines) was processed for an extended period of time without the stimuli being consciously perceived, something that was taken by LR's critics to disconfirm LR. What we found, however, is that LR is not committed to any case of extended processing of information resulting in consciousness, but just when such information is *stable* and/or *actionable*. This will be added to our formulation.

Amendments in hand, we can now formulate three theses of LR:

LR (Main): For all lower-level visual content C, C is conscious if and only if it is stably and actionably represented (in the right way) in recurrent loops

LR (Location-Sufficiency): Recurrent loops between early and mid-level visual areas are sufficient for lower-level visual consciousness

LR (Location-Realizer): Lower-level visual consciousness is typically realized in RP between early and mid-level visual areas, with exceptions occurring only when other means are available for producing RP

While this updated form of LR is more detailed than the one with which we started, it is of course still very general. Nonetheless, it is our resting place for this particular project; it is left to future research to further fill in and modify LR (fleshing out the "in the right way" clause), doing so in response to empirical and theoretical developments.³³

However, before the article's close, there is one more issue to address, one concerning the primary formulation of LR ("LR Main"): Given that it no longer contains the Locational Claim, does this mean that, if the right kind of recurrent loops form in other parts of the brain, e.g., the PFC, this would also give rise to visual consciousness?³⁴ When considering this idea, a good place to start is by remembering that this article restricts its attention to *lower-level* visual consciousness (e.g., brightness, color, shape) (see 1.2), and so the relevant question here would be: If RP (of the right kind) arose that included areas in the PFC, would this give rise *specifically* to some kind of lower-level visual consciousness? This seems unlikely because the PFC does not specialize in processing lower-level kinds of visual content, let alone the copious amount that we find (or at least seem to find) in the average visual experience (Carruthers 2000, Ch. 8; Kozuch 2021). Instead, the PFC produces more complex states (Miyake et al. 2000; Friedman & Robbins 2022), e.g., metacognitive states assessing the reliability of one's perceptions (Vaccaro & Fleming 2018), and it would of course be impossible for activity in a brain area that is not representing a property (e.g., brightness or hue) to be that which constitutes a conscious

³³ One might worry whether the "in the right way" clause could be abused, the worry here being that it might permit all manner of ad hoc modifications to be made to LR so as to save it from falsification. However, the permissibility of any given modification to LR should be considered to be a function of how well-motivated the addition is, with only well-motivated additions—like those made in this article—being considered to save the credibility of LR.

³⁴ I am grateful to an anonymous referee at this journal for having pointed out this issue's importance.

representation of that property.³⁵ At the same time, the possibility of the PFC (or some other brain area) representing large amounts of lower-level visual content can't be ruled out—not without more extended investigation than we have space for here—so this matter is left for another day.

But let's return to the original question again, that of whether RP instantiated in the PFC would produce visual consciousness, this time asking: Even if it didn't produce lower-level visual consciousness, would it produce consciousness of *some* kind? LR, as stated above, seems to imply this. So, if RP were to obtain between, e.g., the dorsolateral PFC and the inferotemporal cortex, LR appears to predict that this would produce some kind of consciousness (probably, a conscious metacognitive state). Whether or not this is the case is another issue going beyond available space. However, it should be pointed out that this entailment is not necessarily to be resisted by the LR Theorist, since a version of LR allowing for this would be well-positioned to account for the multifarious kinds (and seemingly abundant amounts) of content that we appear to find in consciousness: In just the domain of conscious visual content, there are arguably representations of texture, brightness, hue, edges, motion, and perspectival and absolute shape all of which appear to be fine-grained in their detail—along with representations of object identity, and metacognitive states that represent visual perceptions. For each type of conscious visual content, LR could hold that experiences with that type of content are produced whenever the right kind of RP includes whatever brain area(s) specialize in processing that type of content; LR could thereby be able to provide a plausible candidate for producing any of the types of content that we find within consciousness, a candidate that not only produces that type of content, but might also produce it in the seemingly copious quantities that are often found in consciousness (cf. Malach 2021).³⁶ Such, at least, is a sketch of what LR might look like in the future.37

³⁵ This is the *isomorphism constraint* (Noë & Thompson 2004), the idea that "as a matter of nomological necessity, any neural system forming the basis of [experience] E must have the same representational content as E" (Kozuch & Kriegel 2015:403). To grasp the intuitive force of this constraint, consider how odd it would be if activity in a brain area that is not instantiating any representations of color could somehow realize an experience of color.

³⁶ Similar to the view being described currently, Malach takes each kind of visual content to be supplied by the brain area that specializes in processing that type of content, though believes that it is "local ignitions"—quickly ramping up bursts of activity in the brain—that makes such content conscious.

³⁷ This approach is not without liability, since we might come to have reason to think that RP is sometimes simultaneously instantiated in numerous parts of the cortex, in which case it might look as if LR would have to predict that we have *more* content within our typical conscious experience than we appear to actually have. At the same time, once we know more about what is the *right kind* of RP that is sufficient for consciousness, we might find that this limits the amount of content that LR predicts to be conscious to where it is no more than is found in our typical conscious experience.

The ultimate aim of this article has been to see whether, in LR, we have a strong candidate for a Local Theory of consciousness, i.e., a theory that takes activity in the visual cortex to be sufficient for visual consciousness (given certain background conditions), rather than also requiring, e.g., frontoparietal areas. What we have seen in this article is that, not only is there enough data confirming LR to make it look like a viable neuroscientific theory of visual consciousness, but also that all of the data allegedly disconfirming LR can be accommodated by the theory. If we add to this conclusion the mounting evidence against GNW and HO theories that was discussed in the introduction, it seems that LR should be considered to be one of our more promising neuroscientific theories of visual consciousness.

References

Ajina ... Bridge. (2015). Motion area V5/MT+ response to global motion in the absence of V1 resembles early visual cortex. *Brain*, *138*(1), 164–178.

Alkire & Miller. (2005). General anesthesia and the neural correlates of consciousness. *Progress in Brain Research*, *150*, 229–597.

Amassian ... Eberle. (1989). Suppression of visual perception by magnetic coil stimulation of human occipital cortex. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, 74(6), 458–462.

Amassian ... Eberle. (1993). Unmasking human visual perception with the magnetic coil and its relationship to hemispheric asymmetry. *Brain Research*, *605*(2), 312–316.

Amicuzi ... Castelli. (2006). Visual recognition and visually guided action after early bilateral lesion of occipital cortex: A behavioral study of a 4.6-year-old girl. *Neurocase*, *12*(5), 263–279. https://doi.org/10.1080/13554790601026106

Anderson & Rizzo. (1994). Hallucinations following occipital lobe damage: the pathological activation of visual representations. *Journal of Clinical and Experimental Neuropsychology*, *16*(5), 651–663.

Artiga & Sebastián. (2020). Informational theories of content and mental representation. *Review* of *Philosophy and Psychology*, *11*(3), 613–627.

Ashwin & Tsaloumas. (2007). Complex visual hallucinations (Charles Bonnet syndrome) in the hemianopic visual field following occipital infarction. *Journal of the Neurological Sciences*, *263*(1–2), 184–186. https://doi.org/10.1016/j.jns.2007.05.027

Bender ... Sobin. (1968). Palinopsia. Brain: A Journal of Neurology.

Bender & Kahn. (1949). After-imagery in defective fields of vision. *Journal of Neurology, Neurosurgery, and Psychiatry*, *12*(3), 196.

Block. (1996). Mental paint and mental latex. Philosophical Issues, 7, 19-49.

Block. (2005). Two neural correlates of consciousness. *Trends in Cognitive Sciences*, 9(2), 46–52.

Block. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. *Behavioral and Brain Sciences*, *30*(5–6), 481–499.

Block. (2009). Comparing the major theories of consciousness.

Block. (2019). *Empirical science meets higher order views of consciousness: reply to Hakwan Lau and Richard Brown*. MIT Press Cambridge, MA.

Boehler ... Hopf. (2008). Rapid recurrent processing gates awareness in primary visual cortex. *Proceedings of the National Academy of Sciences*, *105*(25), 8742–8747.

Boly ... Tononi. (2017). Are the neural correlates of consciousness in the front or in the back of the cerebral cortex? Clinical and neuroimaging evidence. *Journal of Neuroscience*, *37*(40), 9603–9613.

Bova ... Fazzi. (2008). Recovery of visual functions after early acquired occipital damage. *Developmental Medicine and Child Neurology*, *50*(4), 311–315. https://doi.org/10.1111/j.1469-8749.2008.02044.x

Bridge ... Cowey. (2008). Changes in connectivity after visual cortical brain damage underlie altered visual function. *Brain*, *131*(6), 1433–1444.

Brown ... LeDoux. (2019). Understanding the higher-order approach to consciousness. *Trends in Cognitive Sciences*.

Carmel ... Rees. (2006). Conscious awareness of flicker in humans involves frontal and parietal cortex. *Current Biology*, *16*(9), 907–911.

Center ... Beck. (2019). Examining the role of feedback in TMS-induced visual suppression: A cautionary tale. *Consciousness and Cognition*, *75*, 102805.

Cohen ... Pitts. (2020). Distinguishing the neural correlates of perceptual awareness and postperceptual processing. *Journal of Neuroscience*, 40(25), 4925–4935.

Cowey & Walsh. (2000). Magnetically induced phosphenes in sighted, blind and blindsighted observers. *Neuroreport*, *11*(14), 3269–3273.

Davidson ... Tsuchiya. (2020). The SSVEP tracks attention, not consciousness, during perceptual filling-in. *Elife*, *9*, e60031.

Dehaene & Changeux. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, *70*(2), 200–227.

Dehaene ... Sergent. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences*, *10*(5), 204–211.

Dehaene ... Marti. (2014). Toward a computational theory of conscious processing. *Current Opinion in Neurobiology*, 25, 76–84. https://doi.org/10.1016/j.conb.2013.12.005

Dehaene ... Rivière. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, 4(7), 752–758. https://doi.org/10.1038/89551

Del Cul ... Dehaene. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biology*, *5*(10), 2408–2423. https://doi.org/10.1371/journal.pbio.0050260 Dretske. (1988). *Explaining behavior. Cambridge, MA: Bradford*. MIT Press.

Driver & Vuilleumier. (2001). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*, 79(1-2), 39–88.

Duggal & Pierri. (2002). Charles bonnet syndrome: neurobiological insights. *Indian Journal of Psychiatry*, 44(3), 289–292.

Efron. (1967). The duration of the present. *Annals of the New York Academy of Sciences*, *138*(2), 713–729.

Enns & Lollo. (2000). What's new in visual masking? In *Trends in Cognitive Sciences* (Vol. 4, Issue 9, pp. 345–352). https://doi.org/10.1016/S1364-6613(00)01520-5

Fahrenfort ... Lamme. (2007). Masking disrupts reentrant processing in human visual cortex. *Journal of Cognitive Neuroscience*, *19*(9), 1488–1497.

Fahrenfort ... Lamme. (2012). Neuronal integration in visual cortex elevates face category tuning to conscious face perception. *Proceedings of the National Academy of Sciences*, *109*(52), 21504–21509.

Felleman & Van Essen. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex (New York, NY: 1991)*, *1*(1), 1–47.

Foley. (2015). The case for characterising type-2 blindsight as a genuinely visual phenomenon. *Consciousness and Cognition*, *32*, 56–67.

Friedman & Robbins. (2022). The role of prefrontal cortex in cognitive control and executive function. *Neuropsychopharmacology*, *47*(1), 72–89.

Gaillard ... Naccache. (2009). Converging intracranial markers of conscious access. *PLoS Biology*, 7(3), e1000061.

Ganis. (2013). Visual mental imagery. In *Multisensory imagery* (pp. 9–28). Springer. Genç ... Kohler. (2011). Interhemispheric connections shape subjective experience of bistable motion. *Current Biology*, 21(17), 1494–1499.

Giaschi ... Wong. (2003). Conscious visual abilities in a patient with early bilateral occipital damage. *Developmental Medicine and Child Neurology*, *45*(11), 772–781. https://doi.org/10.1017/S0012162203001439

Gloning ... Hoff. (1967). Uber optische Halluzinationen. Eine Studie an Hand von 241 Patienten mit autoptisch oder chirurgisch verifizierten Läsionen des Okzipitallappens und seiner Grenzgebiete. *Wien Z Nervenheilkd Grenzgeb*, *25*(1), 1–19.

Grafman. (2000). Conceptualizing functional neuroplasticity. *Journal of Communication Disorders*, *33*(4), 345–356.

Grafman ... Wassermann. (2010). Brain damage: Functional reorganization. In *Encyclopedia of Neuroscience* (pp. 327–331). Elsevier Ltd.

Haynes ... Rees. (2005). Visibility reflects dynamic changes of effective connectivity between V1 and fusiform cortex. *Neuron*, *46*(5), 811–821. https://doi.org/10.1016/j.neuron.2005.05.012 Henriksson ... Vanni. (2007). Training-induced cortical representation of a hemianopic hemifield. *Journal of Neurology, Neurosurgery and Psychiatry*, *78*(1), 74–81. https://doi.org/ 10.1136/jnnp.2006.099374

Herzog ... Doerig. (2020). All in good time: long-lasting postdictive effects reveal discrete perception. *Trends in Cognitive Sciences*, *24*(10), 826–837.

Herzog ... Eurich. (2003). Local interactions in neural networks explain global effects in gestalt processing and masking. *Neural Computation*, *15*(9), 2091–2113.

Herzog ... Scharnowski. (2016). Time slices: what is the duration of a percept? *PLoS Biology*, *14*(4), e1002433.

Horton & Hoyt. (1991). Quadrantic visual field defects: a hallmark of lesions in extrastriate (V2/V3) cortex. *Brain*, *114*(4), 1703–1718.

Hurme ... Railo. (2019). V1 activity during feedforward and early feedback processing is necessary for both conscious and unconscious motion perception. *NeuroImage*, *185*, 313–321. Jackson. (2003). Mind and illusion. *Royal Institute of Philosophy Supplements*, *53*, 251–271. Jacob & de Vignemont. (2010). Spatial coordinates and phenomenology in the two-visual systems model. *Perception, Action, and Consciousness: Sensorimotor Dynamics and Two-Visual*

Systems, 125–144.

Jehle & Kriegel. (2006). An argument against dispositionalist HOT theory. *Philosophical Psychology*, *19*(4), 463–476.

Jiang ... He. (2007). Human visual cortex responds to invisible chromatic flicker. *Nature Neuroscience*, *10*(5), 657–662.

Jolij & Lamme. (2005). Repression of unconscious information by conscious processing: Evidence from affective blindsight induced by transcranial magnetic stimulation. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(30), 10747–10751. https://doi.org/10.1073/pnas.0500834102

Kaas. (2013). The evolution of brains from early mammals to humans. *Wiley Interdisciplinary Reviews: Cognitive Science*, *4*(1), 33–45.

Kleiser ... Stoerig. (2001). Is V1 necessary for conscious vision in areas of relative cortical blindness? *Neuroimage*, *13*(4), 654–661.

Koivisto ... Revonsuo. (2017). Transcranial magnetic stimulation of early visual cortex suppresses conscious representations in a dichotomous manner without gradually decreasing their precision. *NeuroImage*, *158*, 308–318. https://doi.org/10.1016/j.neuroimage.2017.07.011 Koivisto ... Salminen-Vaparanta. (2011). Transcranial magnetic stimulation of early visual cortex interferes with subjective visual awareness and objective forced-choice performance. *Consciousness and Cognition*, *20*(2), 288–298. https://doi.org/10.1016/j.concog.2010.09.001 Kölmel. (1985). Complex visual hallucinations in the hemianopic field. *Journal of Neurology, Neurosurgery & Psychiatry*, *48*(1), 29–38.

Kozuch. (2014). Prefrontal lesion evidence against higher-order theories of consciousness. *Philosophical Studies*, *167*(3), 721–746.

Kozuch. (2015). Dislocation, not dissociation: The neuroanatomical argument against visual experience driving motor action. *Mind & Language*, *30*(5), 572–602.

Kozuch. (2021). Underwhelming force: Evaluating the neuropsychological evidence for higherorder theories of consciousness. *Mind & Language*. https://doi.org/10.1111/mila.12363

Kozuch. (2022). Conscious vision guides motor action—rarely. *Philosophical Psychology*, 1–34. Kozuch & Kriegel. (2015). Correlation, Causation, Constitution: On the Interplay between the Science and Philosophy of Consciousness. In S. M. Miller (Ed.), *The Constitution of*

Phenomenal Consciousness (pp. 400-417). John Benjamins.

Kriegel. (2007a). Consciousness: Phenomenal consciousness, access consciousness, and scientific practice. In *Philosophy of Psychology and Cognitive Science* (pp. 195–217). Elsevier.

Kriegel. (2007b). The phenomenologically manifest. *Phenomenology and the Cognitive Sciences*, 6(1–2), 115–136.

Lamme. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, 7(1), 12–18.

Lamme. (2004). Separate neural definitions of visual consciousness and visual attention; a case for phenomenal awareness. *Neural Networks*, *17*(5–6), 861–872.

Lamme. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*(11), 494–501.

Lamme. (2010). How neuroscience will change our view on consciousness. *Cognitive Neuroscience*, *1*(3), 204–220. https://doi.org/10.1080/17588921003731586

Lamme. (2015). The Crack of Dawn - Perceptual Functions and Neural Mechanisms that Mark the Transition from Unconscious Processing to Conscious Vision. In *Open MIND* (Vol. 22). https://open-mind.net/papers/the-crack-of-dawn-perceptual-functions-and-neural-mechanismsthat-mark-the-transition-from-unconscious-processing-to-conscious-vision/at_download/ paperPDF

Lamme & Roelfsema. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, 23(11), 571–579.

Lamme ... Spekreijse. (2002). Masking interrupts figure-ground signals in V1. *Journal of Cognitive Neuroscience*, *14*(7), 1044–1053.

Lau & Brown. (2019). The Emperor's New Phenomenology? The Empirical Case for Conscious Experiences without First-Order Representations. In A. Pautz & D. Stoljar (Eds.), *Blockheads! Essavs on Ned Block's philosophy of mind and consciousness* (pp. 199–213). MIT.

Lau & Rosenthal. (2011). Empirical support for higher-order theories of conscious awareness. *Trends in Cognitive Sciences*, *15*(8), 365–373.

Macknik & Martinez-Conde. (2007). The role of feedback in visual masking and visual processing. *Advances in Cognitive Psychology*, *3*(1–2), 125.

Malach. (2021). Local neuronal relational structures underlying the contents of human conscious experience. *Neuroscience of Consciousness*, 2021(2), niab028.

Marcel. (1998). Blindsight and shape perception: deficit of visual consciousness or of visual function? *Brain: A Journal of Neurology*, *121*(8), 1565–1588.

Marois ... Chun. (2004). The Neural Fate of Consciously Perceived and Missed Events in the Attentional Blink. *Neuron*, *41*(3), 465–472. https://doi.org/10.1016/S0896-6273(04)00012-1 Mashour ... Dehaene. (2020). Conscious Processing and the Global Neuronal Workspace Hypothesis. In *Neuron* (Vol. 105, Issue 5, pp. 776–798). https://doi.org/10.1016/j.neuron.2020.01.026

Masur ... Oberwittler. (1993). Suppression of visual perception by transcranial magnetic stimulation—experimental findings in healthy subjects and patients with optic neuritis. *Electroencephalography and Clinical Neurophysiology*, *86*(4), 259–267.

Mazzi ... Silvanto. (2019). On the "blindness" of blindsight: What is the evidence for phenomenal awareness in the absence of primary visual cortex (V1)? *Neuropsychologia*, *128*, 103–108.

McCarthy & Warrington. (1986). Visual associative agnosia: a clinico-anatomical study of a single case. *Journal of Neurology, Neurosurgery & Psychiatry*, 49(11), 1233–1240.

McFadzean & Hadley. (1997). Homonymous quadrantanopia respecting the horizontal meridian: A feature of striate and extrastriate cortical disease. *Neurology*, *49*(6), 1741–1746.

Merigan & Maunsell. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*(1), 369–402.

Michel & Doerig. (2021). A new empirical challenge for local theories of consciousness. *Mind & Language*.

Michel & Morales. (2020). Minority reports: Consciousness and the prefrontal cortex. *Mind & Language*, *35*(4), 493–513.

Miyake ... Wager. (2000). The unity and diversity of executive functions and their contributions to complex "frontal lobe" tasks: A latent variable analysis. *Cognitive Psychology*, *41*(1), 49–100. Morales & Lau. (2020). The Neural Correlates of Consciousness. In *Oxford Handbook of the Philosophy of Consciousness*. OUP.

Muckli ... Singer. (2009). Bilateral visual field maps in a patient with only one hemisphere. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(31), 13034–13039. https://doi.org/10.1073/pnas.0809688106

Noë & Thompson. (2004). Are there neural correlates of consciousness? *Journal of Consciousness Studies*, *11*(1), 3–28.

Oizumi ... Tononi. (2014). From the phenomenology to the mechanisms of consciousness: integrated information theory 3.0. *PLoS Computational Biology*, *10*(5), e1003588.

Papineau. (2021). The metaphysics of sensory experience. Oxford University Press.

Pascual-Leone & Walsh. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science*, *292*(5516), 510–512.

Pitts ... Hillyard. (2012). Visual processing of contour patterns under conditions of inattentional blindness. *Journal of Cognitive Neuroscience*, *24*(2), 287–303. https://doi.org/10.1162/jocn_a_00111

Polack & Contreras. (2012). Long-range parallel processing and local recurrent activity in the visual cortex of the mouse. *Journal of Neuroscience*, *32*(32), 11120–11131.

Pollen. (1999). On the neural correlates of visual perception. Cerebral Cortex, 9(1), 4–19.

Pollen. (2007). Fundamental requirements for primary visual perception. *Cerebral Cortex*, 18(9), 1991–1998.

Raccah ... Fox. (2021). Does the Prefrontal Cortex Play an Essential Role in Consciousness? Insights from Intracranial Electrical Stimulation of the Human Brain. *The Journal of*

Neuroscience, *41*(10), 2076–2087. https://doi.org/10.1523/JNEUROSCI.1141-20.2020 Railo & Koivisto. (2012). Two means of suppressing visual awareness: A direct comparison of visual masking and transcranial magnetic stimulation. *Cortex*, *48*(3), 333–343. https://doi.org/ 10.1016/j.cortex.2010.12.001

Rees ... Koch. (2002). Neural correlates of consciousness in humans. *Nature Reviews Neuroscience*, *3*(4), 261–270.

Riddoch. (1917). Dissociation of visual perceptions due to occipital injuries, with especial reference to appreciation of movement. *Brain*, 40(1), 15–57.

Riedel ... Brandt. (2004). Areas MT/V5 and their transcallosal connectivity in cortical dysplasia by fMRI. *Neuroreport*, *15*(12), 1877–1881.

Ro ... Lane. (2003). Feedback contributions to visual awareness in human occipital cortex. *Current Biology*, *13*(12), 1038–1041.

Sahraie ... Brammer. (1997). Pattern of neuronal activity associated with conscious and unconscious processing of visual signals. *Proceedings of the National Academy of Sciences*, *94*(17), 9406–9411.

Salminen-Vaparanta ... Revonsuo. (2012). Neuronavigated transcranial magnetic stimulation suggests that area V2 is necessary for visual awareness. *Neuropsychologia*, *50*(7), 1621–1627. Scharnowski ... Herzog. (2009). Long-lasting modulation of feature integration by transcranial magnetic stimulation. *Journal of Vision*, *9*(6), 1.

Schölvinck & Rees. (2010). Neural correlates of motion-induced blindness in the human brain. *Journal of Cognitive Neuroscience*, *22*(6), 1235–1243.

Sergent ... Dehaene. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nature Neuroscience*, 8(10), 1391–1400. https://doi.org/10.1038/ nn1549

Siegel & Byrne. (2017). Rich or thin? In *Current controversies in philosophy of perception* (pp. 59–80). Routledge.

Silvanto. (2015). Why is "blindsight" blind? A new perspective on primary visual cortex, recurrent activity and visual awareness. *Consciousness and Cognition*, *32*, 15–32.

Silvanto ... Walsh. (2007). Making the blindsighted see. *Neuropsychologia*, 45(14), 3346–3350. Silvanto ... Walsh. (2008). Inducing conscious perception of colour in blindsight. *Current Biology*, 18(20), R950–R951.

Silvanto ... Walsh. (2005). Double dissociation of V1 and V5/MT activity in visual awareness. *Cerebral Cortex*, *15*(11), 1736–1741. https://doi.org/10.1093/cercor/bhi050

Silvanto & Rees. (2011). What does neural plasticity tell us about role of primary visual cortex (V1) in visual awareness? *Frontiers in Psychology*, 2(6), 1–5. https://doi.org/10.3389/fpsyg.2011.00006

Stoerig. (2001). The neuroanatomy of phenomenal vision: a psychological perspective. *Annals of the New York Academy of Sciences*, 929(1), 176–194.

Stoerig & Cowey. (1995). Visual perception and phenomenal consciousness. *Behavioural Brain Research*, *71*(1–2), 147–156.

Stoerig & Cowey. (1997). Blindsight in man and monkey. *Brain: A Journal of Neurology*, *120*(3), 535–559.

Teuber ... Bender. (1960). *Visual field defects after penetrating missile wounds of the brain*. Harvard University Press.

Tononi. (2004). An information integration theory of consciousness. *BMC Neuroscience*, 5(1), 1–22.

Torjussen. (1976). Residual function in cortically blind hemifields. *Scandinavian Journal of Psychology*, *17*(1), 320–322.

Van Essen & Anderson. (1995). Information processing strategies and pathways in the primate visual system. *An Introduction to Neural and Electronic Networks*, *2*, 45–76.

Van Gaal & Lamme. (2012). Unconscious high-level information processing: implication for neurobiological theories of consciousness. *The Neuroscientist*, *18*(3), 287–301.

Van Vugt ... Roelfsema. (2018). The threshold for conscious report: Signal loss and response bias in visual and frontal cortex. *Science*, *360*(6388), 537–542.

Varela ... Martinerie. (2001). The brainweb: phase synchronization and large-scale integration. *Nature Reviews Neuroscience*, *2*(4), 229–239.

Voytek ... Knight. (2010). *Dynamic neuroplasticity after human prefrontal cortex damage*. *68*(3), 401–408.

Vuilleumier ... Gabrieli. (2001). Neural fate of seen and unseen faces in visuospatial neglect: A combined event-related functional MRI and event-related potential study. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(6), 3495–3500. https://doi.org/10.1073/pnas.051436898

Warrington. (1962). The completion of visual forms across hemianopic field defects. *Journal of Neurology, Neurosurgery, and Psychiatry*, 25(3), 208.

Warrington. (1965). The effect of stimulus configuration on the incidence of the completion phenomenon. *British Journal of Psychology*, *56*(4), 447–454.

Weiskrantz. (1996). Blindsight revisited. *Current Opinion in Neurobiology*, 6(2), 215–220. Weiskrantz ... Sahraie. (1995). Parameters affecting conscious versus unconscious visual discrimination with damage to the visual cortex (V1). *Proceedings of the National Academy of Sciences*, *92*(13), 6122–6126.

Wyart ... Tallon-Baudry. (2012). Early dissociation between neural signatures of endogenous spatial attention and perceptual awareness during visual masking. *Frontiers in Human Neuroscience*, *6*, 16.

Zeki. (2003). The disunity of consciousness. *Trends in Cognitive Sciences*, 7(5), 214–218. Zeki & Bartels. (1999). Toward a theory of visual consciousness. *Consciousness and Cognition*, 8(2), 225–259.

Zeki & Ffytche. (1998). The Riddoch syndrome: insights into the neurobiology of conscious vision. *Brain: A Journal of Neurology*, *121*(1), 25–45.

Zou ... Zhang. (2016). Binocular rivalry from invisible patterns. *Proceedings of the National Academy of Sciences*, *113*(30), 8408–8413.