frontiers
RESEARCH TOPICS

INVISIBLE, BUT HOW? THE DEPTH OF UNCONSCIOUS PROCESSING AS INFERRED FROM DIFFERENT SUPPRESSION TECHNIQUES

Topic Editors
Julien Dubois and Nathan Faivre

frontiers in
PSYCHOLOGY

FRONTIERS COPYRIGHT STATEMENT

Cover image provided by Ibbl sarl, Lausanne CH

ISSN 1664-8714
ISBN 978-2-88919-420-9
DOI 10.3389/978-2-88919-420-9

ABOUT FRONTIERS

Frontiers is more than just an open-access publisher of scholarly articles: it is a pioneering approach to the world of academia, radically improving the way scholarly research is managed. The grand vision of Frontiers is a world where all people have an equal opportunity to seek, share and generate knowledge. Frontiers provides immediate and permanent online open access to all its publications, but this alone is not enough to realize our grand goals.

FRONTIERS JOURNAL SERIES

The Frontiers Journal Series is a multi-tier and interdisciplinary set of open-access, online journals, promising a paradigm shift from the current review, selection and dissemination processes in academic publishing.

All Frontiers journals are driven by researchers for researchers; therefore, they constitute a service to the scholarly community. At the same time, the Frontiers Journal Series operates on a revolutionary invention, the tiered publishing system, initially addressing specific communities of scholars, and gradually climbing up to broader public understanding, thus serving the interests of the lay society, too.

DEDICATION TO QUALITY

Each Frontiers article is a landmark of the highest quality, thanks to genuinely collaborative interactions between authors and review editors, who include some of the world's best academicians. Research must be certified by peers before entering a stream of knowledge that may eventually reach the public - and shape society; therefore, Frontiers only applies the most rigorous and unbiased reviews.

Frontiers revolutionizes research publishing by freely delivering the most outstanding research, evaluated with no bias from both the academic and social point of view.

By applying the most advanced information technologies, Frontiers is catapulting scholarly publishing into a new generation.

WHAT ARE FRONTIERS RESEARCH TOPICS?

Frontiers Research Topics are very popular trademarks of the Frontiers Journals Series: they are collections of at least ten articles, all centered on a particular subject. With their unique mix of varied contributions from Original Research to Review Articles, Frontiers Research Topics unify the most influential researchers, the latest key findings and historical advances in a hot research area!

Find out more on how to host your own Frontiers Research Topic or contribute to one as an author by contacting the Frontiers Editorial Office: researchtopics@frontiersin.org

INVISIBLE, BUT HOW? THE DEPTH OF UNCONSCIOUS PROCESSING AS INFERRED FROM DIFFERENT SUPPRESSION TECHNIQUES

Topic Editor:
Julien Dubois, California Institute of Technology, USA
Nathan Faivre, California Institute of Technology, USA

To what level are invisible stimuli processed by the brain in the absence of conscious awareness? It is widely accepted that simple visual properties of invisible stimuli are processed; however, the existence of higher-level unconscious processing (e.g., involving semantic or executive functions) remains a matter of debate. Several methodological factors may underlie the discrepancies found in the literature, such as different levels of conservativeness in the definition of "unconscious" or different dependent measures of unconscious processing. In this research topic, we are particularly interested in yet another factor: inherent differences in the amount of information let through by different suppression techniques. In the same conditions of well-controlled, conservatively established invisibility, can we show that some of the techniques in the "psychophysical magic" arsenal (e.g., masking, but also visual crowding, attentional blink, etc.) reliably lead to higher-level unconscious processing than others (e.g., interocular suppression)? Some authors have started investigating this question, using multiple techniques in similar settings . We argue that this approach should be extended and refined. Indeed, in order to delineate the frontiers of the unconscious mind using a contrastive method, one has to disentangle the limits attributable to unawareness itself, and those attributable to the technique inducing unawareness. The scope of this research topic is to provide a platform for scientists to contribute insights and further experiments addressing this fundamental question.

Table of Contents

04 ***Invisible, but how? The Depth of Unconscious Processing as Inferred From Different Suppression Techniques***
Julien Dubois and Nathan Faivre

07 ***Elucidating Unconscious Processing with Instrumental Hypnosis***
Mathieu Landry, Krystèle Appourchaux and Amir Raz

25 ***On the Use of Continuous Flash Suppression for the Study of Visual Processing Outside of Awareness***
Eunice Yang, Jan Brascamp, Min-Suk Kang and Randolph Blake

42 ***Breaking Continuous Flash Suppression: Competing for Consciousness on the Pre-Semantic Battlefield***
Surya Gayet, Stefan Van Der Stigchel and Chris L. E. Paffen

52 ***Unconscious Processing Under Interocular Suppression: Getting the Right Measure***
Timo Stein and Philipp Sterzer

57 ***Neural Processing of Visual Information Under Interocular Suppression: A Critical Review***
Philipp Sterzer, Timo Stein, Karin Ludwig, Marcus Rothkirch and Guido Hesselmann

69 ***Sustained Invisibility through Crowding and Continuous Flash Suppression: A Comparative Review***
Nathan Faivre, Vincent Berthet and Sid Kouider

82 ***Invisibility and Interpretation***
Michael H. Herzog, Frouke Hermens and Haluk Ogmen

91 ***Evidence of Weak Conscious Experiences in the Exclusion Task***
Kristian Sandberg, Simon H. Del Pin, Bo M. Bibby and Morten Overgaard

99 ***Waves of Visibility: Probing the Depth of Inter-Ocular Suppression with Transient and Sustained Targets***
Lisandro N. Kaunitz, Alessio Fracasso, Maris Skujevskis and David Melcher

109 ***Comparing Unconscious Processing During Continuous Flash Suppression and Meta-Contrast Masking Just Under the Limen of Consciousness***
Ziv Peremen and Dominique Lamy

122 ***A Direct Comparison of Unconscious Face Processing Under Masking and Interocular Suppression***
Gregory Izatt, Julien Dubois, Nathan Faivre and Christof Koch

133 ***Unconscious Neural Processing Differs with Method Used to Render Stimuli Invisible***
Sergey V. Fogelson, Peter J. Kohler, Kevin J. Miller, Richard Granger and Peter U. Tse

frontiers in
PSYCHOLOGY

EDITORIAL
published: 01 October 2014
doi: 10.3389/fpsyg.2014.01117

Invisible, but how? The depth of unconscious processing as inferred from different suppression techniques

Julien Dubois* and Nathan Faivre

Division of Biology, California Institute of Technology, Pasadena, CA, USA
**Correspondence: jcrdubois@gmail.com*

Edited and reviewed by:
Anil K. Seth, University of Sussex, UK

Keywords: unconscious processing, Continuous Flash Suppression (CFS), backward masking, visual crowding, invisibility, measures of consciousness, interocular suppression, psychophysical magic

To what level are invisible stimuli processed by the brain in the absence of conscious awareness? Taking stock of the evidence to this day, it is widely accepted that simple visual properties of invisible stimuli are processed; however, the existence of higher-level unconscious processing (e.g., involving semantic or executive functions) remains a matter of debate. After several years of research in the field of unconscious processing, we became aware of a number of methodological aspects which need to be controlled carefully to help resolve discrepant findings in the literature. These aspects relate to: (1) when and how visibility is assessed; (2) when and how unconscious processing is assessed; (3) whether spatiotemporal attention is directed or, at least, measured; (4) whether adequate control conditions are used to rule out alternate explanations; (5) whether the studies are sufficiently powered and account for individual differences. Yet even when these aspects are carefully controlled, there may be, and probably are, some inherent differences in the amount of information let through by the different invisibility-inducing techniques (the "psychophysical magic" arsenal, Kim and Blake, 2005). We launched this Research Topic to foster investigations into these inherent differences (note previous attempts, Breitmeyer et al., 2004; Almeida et al., 2008; Kanai et al., 2010; Faivre et al., 2012).

The articles in this issue span various aspects of the research question that we put out to the community.

Perhaps the best starting point for a thorough introduction to the field of unconscious processing is the contribution by Landry et al. (2014): they review the different techniques used to prevent visual awareness, emphasizing the distinction between subliminal vs. preconscious processing, and find difficulty in reconciling the variety of techniques and results in the literature. They advocate the use of hypnosis, a top-down approach that can induce both perceptual and attentional failures, as a way to bridge the existing gap in the literature.

Continuous Flash Suppression (CFS) (Tsuchiya and Koch, 2005; Tsuchiya et al., 2006) consists in presenting a low contrast target stimulus to one eye while flashing a stream of high contrast stimuli to the other eye, resulting in strong interocular suppression. This rather young technique (as compared to masking or binocular rivalry) has boosted the field of unconscious processing in the past 10 years, allowing researchers to render stimuli invisible for seconds at a time in a very robust fashion. A slight but significant twist referred to as "breaking Continuous Flash Suppression" (bCFS) (Jiang et al., 2007), which consists in comparing the time it takes for different stimuli to break suppression, has been in the spotlight recently. Using bCFS, researchers have claimed that many high-level properties of invisible stimuli are processed unconsciously, which clashes with classical results from binocular rivalry and CFS itself. Yang et al. (2014) offer an insightful review of behavioral CFS and bCFS findings. Though they conclude that the emerging picture is that extensive processing can occur under CFS, they caution against many common issues in the use of (b)CFS. Gayet et al. (2014) focus exclusively on bCFS, and review the 30 studies published to date using this technique. They reject most conclusions of high-level processing, arguing that low-level mechanisms could account for the data. In a similar vein (Stein and Sterzer, 2014) argue that bCFS is not a valid measure of consciousness in its current implementation, and propose some modifications to the paradigm. Taking a step back from the controversies about bCFS (Sterzer et al., 2014) review neural processing under interocular suppression. They conclude that the literature currently presents highly heterogeneous findings regarding which structures are involved in processing suppressed stimuli and which stimuli can be processed; they emphasize the importance of controlling the depth of suppression in future studies, and advocate the use of online, continuous measures that capture the functional relevance of brain signals related to the processing of invisible stimuli. Finally (Faivre et al., 2014) compare published findings in the CFS and visual crowding literatures, as two methods designed to induce sustained invisibility. They conclude that the literature does not yet provide a coherent picture on the extent of processing under each of the two methods.

Taken together, these six review and opinion articles paint an accurate picture of the current landscape and controversies around unconscious processing. In addition, we received six original research articles.

A crucial choice in unconscious processing studies is that of the measure to establish invisibility, and there is still considerable debate on what this measure should be. This is illustrated in a contribution by Herzog et al. (2014), in which the very notion of invisibility is challenged, and reformulated in terms of a purposeful interpretation (i.e., spatiotemporal grouping) of incoming stimuli by the brain. In this view, the features of incoming stimuli are always visible and available to the brain, it is just a matter of how they are interpreted. Based on a more traditional definition of invisibility (Sandberg et al., 2014) compare exclusion tasks, in which participants are asked to solve an experimental task without using information from the invisible stimulus, with subjective visibility measures, in which participants are asked to indicate their subjective experience on a perceptual awareness scale (PAS). They find that exclusion tasks may in fact be a less sensitive and exhaustive measure of awareness than the PAS.

Another important choice in unconscious processing studies is what exact parameters should be used, within a given technique, to create the conditions of invisibility that one wishes to work with. Kaunitz et al. (2014) investigate the role of various parameters (onset time of the stimulus with respect to the onset of the masks, mask frequency, number of masks, duration of the stimulus) for the masking of a brief target stimulus with CFS. They notably find that showing a number of masks before the target does not increase suppression depth, and that a higher temporal frequency of Mondrian presentation results in deeper suppression. Their study demonstrates the importance of small, often overlooked, experimental details which can have an impact on the outcome of different studies and prevent comparison of results.

Finally, we received three studies comparing the extent of unconscious processing under different suppression techniques, either at a behavioral or at a neural level. Peremen and Lamy (2014) compare priming for directional arrow stimuli under metacontrast masking and CFS, in two separate experiments. They find that priming occurs with metacontrast masking but is abolished when stimuli are rendered invisible with CFS. They use each technique as it is optimally implemented, meaning that a number of experimental factors differ between the two experiments (as in Almeida et al., 2008, 2010). Izatt et al. (2014) also chose to compare masking and interocular suppression, but with a fame priming paradigm using invisible faces. The authors take great care to equate most experimental parameters and randomly present both techniques within the same experiment, such that the subjects are completely unaware of which is used on any given trial. Under these conditions, the authors do not find significant differences in the processing of faces rendered invisible by the two techniques, but they generally observe that priming effects are larger with masking than interocular suppression. Last (Fogelson et al., 2014) render a small set of four faces and four tools invisible using two techniques that allow sustained invisibility: CFS, and the less common chromatic flicker fusion (CFF). They concurrently record fMRI and, under the same condition of invisibility, attempt to decode the category of the invisible stimuli throughout the brain. They find that informative regions differ between the two techniques.

These contributions bring valuable insights into the question that we set out to address when we launched this Research Topic. This is a strong starting point to an in-depth systematic comparison of measures and techniques in the study of unconscious vision. We sincerely hope that the readers will find this collection of articles as stimulating and thought-provoking as we do, and that they will apply some of the many wise recommendations interspersed throughout to their own line of research.

ACKNOWLEDGMENT

We thank Liad Mudrik for helpful comments on this manuscript.

REFERENCES

Almeida, J., Mahon, B. Z., and Caramazza, A. (2010). The role of the dorsal visual processing stream in tool identification. *Psychol. Sci.* 21, 772–778. doi: 10.1177/0956797610371343

Almeida, J., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proc. Natl. Acad. Sci.* 105, 15214–15218. doi: 10.1073/pnas.0805867105

Breitmeyer, B. G., Ro, T., and Ogmen, H. (2004). A comparison of masking by visual and transcranial magnetic stimulation: implications for the study of conscious and unconscious visual processing. *Conscious. Cogn.* 13, 829–843. doi: 10.1016/j.concog.2004.08.007

Faivre, N., Berthet, V., and Kouider, S. (2012). Nonconscious influences from emotional faces: a comparison of visual crowding, masking, and continuous flash suppression. *Front. Psychol.* 3:129. doi: 10.3389/fpsyg.2012.00129

Faivre, N., Berthet, V., and Kouider, S. (2014). Sustained invisibility through crowding and continuous flash suppression: a comparative review. *Front. Psychol.* 5:475. doi: 10.3389/fpsyg.2014.00475

Fogelson, S. V., Kohler, P. J., Miller, K. J., Granger, R., and Tse, P. U. (2014). Unconscious neural processing differs with method used to render stimuli invisible. *Front. Psychol.* 5:601. doi: 10.3389/fpsyg.2014.00601

Gayet, S., Van der Stigchel, S., and Paffen, C. L. E. (2014). Breaking continuous flash suppression: competing for consciousness on the pre-semantic battlefield. *Front. Psychol.* 5:460. doi: 10.3389/fpsyg.2014.00460

Herzog, M., Hermens, F., and Ogmen, H. (2014). Invisibility & Interpretation. *Front. Psychol.* 5:975. doi: 10.3389/fpsyg.2014.00975

Izatt, G., Dubois, J., Faivre, N., and Koch, C. (2014). A direct comparison of unconscious face processing under masking and interocular suppression. *Front. Psychol.* 5, 1–11. doi: 10.3389/fpsyg.2014.00659

Jiang, Y., Costello, P., and He, S. (2007). Processing of invisible stimuli: advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychol. Sci.* 18, 349–355. doi: 10.1111/j.1467-9280.2007.01902.x

Kanai, R., Walsh, V., and Tseng, C. (2010). Subjective discriminability of invisibility: a framework for distinguishing perceptual and attentional failures of awareness. *Conscious. Cogn.* 19, 1045–1057. doi: 10.1016/j.concog.2010.06.003

Kaunitz, L. N., Fracasso, A., Skujevskis, M., and Melcher, D. (2014). Waves of visibility: probing the depth of inter-ocular suppression with transient and sustained targets. *Front. Psychol.* 5, 1–10. doi: 10.3389/fpsyg.2014.00804

Kim, C.-Y., and Blake, R. (2005). Psychophysical magic: rendering the visible "invisible". *Trends Cogn. Sci.* 9, 381–388. doi: 10.1016/j.tics.2005.06.012

Landry, M., Appourchaux, K., and Raz, A. (2014). Elucidating unconscious processing with instrumental hypnosis. *Front. Psychol.* 5, 1–18. doi: 10.3389/fpsyg.2014.00785

Peremen, Z., and Lamy, D. (2014). Comparing unconscious processing during continuous flash suppression and meta-contrast masking just under the limen of consciousness. *Front. Psychol.* 5:969. doi: 10.3389/fpsyg.2014.00969

Sandberg, K., Del Pin, S. H., Bibby, B. M., and Overgaard, M. (2014). Evidence of weak conscious experiences in the exclusion task. *Front. Psychol.* 5, 1080. doi: 10.3389/fpsyg.2014.01080

Stein, T., and Sterzer, P. (2014). Unconscious processing under interocular suppression: getting the right measure. *Front. Psychol.* 5:387. doi: 10.3389/fpsyg.2014.00387

Sterzer, P., Stein, T., Ludwig, K., Rothkirch, M., and Hesselmann, G. (2014). Neural processing of visual information under interocular suppression: a critical review. *Front. Psychol.* 5:453. doi: 10.3389/fpsyg.2014.00453

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Tsuchiya, N., Koch, C., Gilroy, L. A., and Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *J. Vis.* 6, 1068–1078. doi: 10.1167/6.10.6

Yang, E., Brascamp, J., Kang, M.-S., and Blake, R. (2014). On the use of continuous flash suppression for the study of visual processing outside of awareness. *Front. Psychol.* 5:724. doi: 10.3389/fpsyg.2014.00724

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 08 September 2014; accepted: 15 September 2014; published online: 01 October 2014.

Citation: Dubois J and Faivre N (2014) Invisible, but how? The depth of unconscious processing as inferred from different suppression techniques. Front. Psychol. ***5****:1117. doi: 10.3389/fpsyg.2014.01117*

This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

HYPOTHESIS AND THEORY ARTICLE
published: 28 July 2014
doi: 10.3389/fpsyg.2014.00785

Elucidating unconscious processing with instrumental hypnosis

Mathieu Landry[1], Krystèle Appourchaux[2] and Amir Raz[2,3] *

[1] Integrated Program in Neuroscience, McGill University, Montreal, QC, Canada
[2] Department of Psychiatry, McGill University, Montreal, QC, Canada
[3] Lady Davis Institute for Medical Research, Jewish General Hospital, Montreal, QC, Canada

Edited by:
Nathan Faivre, California Institute of Technology, USA

Reviewed by:
Peter Halligan, Cardiff University, UK
Chai-Youn Kim, Korea University, Korea (South)
Rochelle Cox, Macquarie University, Australia

***Correspondence:**
Amir Raz, Department of Psychiatry, McGill University, 4333 Cote-Sainte-Catherine Road, Montreal, QC H3T 1E4, Canada
e-mail: amir.raz@mcgill.ca

Most researchers leverage bottom-up suppression to unlock the underlying mechanisms of unconscious processing. However, a top-down approach – for example via hypnotic suggestion – paves the road to experimental innovation and complementary data that afford new scientific insights concerning attention and the unconscious. Drawing from a reliable taxonomy that differentiates subliminal and preconscious processing, we outline how an experimental trajectory that champions top-down suppression techniques, such as those practiced in hypnosis, is uniquely poised to further contextualize and refine our scientific understanding of unconscious processing. Examining subliminal and preconscious methods, we demonstrate how instrumental hypnosis provides a reliable adjunct that supplements contemporary approaches. Specifically, we provide an integrative synthesis of the advantages and shortcomings that accompany a top-down approach to probe the unconscious mind. Our account provides a larger framework for complementing the results from core studies involving prevailing subliminal and preconscious techniques.

Keywords: unconscious, instrumental hypnosis, suggestion, subliminal perception, preconscious processing, suppression of consciousness, consciousness, global workspace

INTRODUCTION

The unconscious mind fascinates and challenges human thinking (Tallis, 2002). Pervasive even in popular science (Mlodinow, 2012), the so-called "new" unconscious shares in the innovations and advances of consciousness research (Dehaene et al., 2006; Kouider and Dehaene, 2007; Seth et al., 2008; Dehaene, 2011; Dehaene and Changeux, 2011). This fast-growing field offers novel perspectives concerning the powerful influence of the unconscious mind on thought and behavior (Hassin et al., 2005). In the quest to understand the unconscious realm, various psychophysical techniques that suppress conscious access to sensory events largely frame our insights regarding the depth of unconscious processing and serve as a robust methodological backbone (Kim and Blake, 2005). Yet, despite such valuable methods, inconsistencies across tasks fuel a conundrum regarding the depth of processing of the cognitive unconscious – unconscious mental structures and processes that support thoughts and behaviors (Kihlstrom, 1987). These inconsistencies not only call for caution when generalizing results from a single family of similar tasks, but also suggest that suppression mechanisms are mostly task-dependent (Tsuchiya et al., 2006; Faivre et al., 2014; Fogelson et al., 2014; Izatt et al., 2014). In their attempt to identify the underlying mechanisms subserving unconscious processing, researchers increasingly seek to diversify their critical inquiry. Here we draw upon the science of hypnosis – a technique with a long track record of study concerning the unconscious – and show how it can become a useful vehicle to complement and diversify existing empirical approaches.

Recovering from a volatile history plagued by quackery and charlatanism, hypnosis has become a viable venue of cognitive science (Oakley and Halligan, 2009, 2013; Raz, 2011b). At least in part, this interest owes to the potent influence hypnotic and post-hypnotic suggestions wield over sensory, cognitive, and motor processing (Nash and Barnier, 2008). Relying on such findings, we argue that research on the cognitive unconscious would benefit from including hypnosis paradigms. Complementing current assortment of suppression techniques with the powerful effects of hypnosis affords researchers with a distinctive mean to test novel hypotheses about unconscious processing.

Using hypnosis in the study of the unconscious mind dates back to early psychodynamic conceptions when analysts leveraged hypnotism to probe unconscious thoughts and feelings of analysands (Bachner-Melman and Lichtenberg, 2001). Revisiting this idea, hypnosis research informs our scientific views of the cognitive unconscious, mental processes, and their structure (Kihlstrom, 1987). Here we draw on this framework and outline how instrumental hypnosis – i.e., the instrumental use of hypnotic suggestions to explore the underlying mechanisms of typical and atypical cognition – promises to make way for a top-down approach in the study of unconscious processes. Specifically, this top-down approach aims to harness the effects of higher cognitive functions upon lower level processing. We argue that instrumental hypnosis paves the road to multiple methodological advances in the exploration of the unconscious mind. We differentiate between subliminal and preconscious approaches (Dehaene et al., 2006; Dehaene, 2011), whereby the former reflects perceptual failures and the latter attentional failures (Kanai et al., 2010). We will explain how hypnotic suggestions can exploit the mechanisms of suppression and inattention to unravel unconscious processes. Importantly, this innovative framework does not champion top-down over bottom-up approaches, but rather advocates exploiting both approaches together to better unravel the complexity of unconscious processing.

We review contemporary suppression and inattention techniques to assess their relative merits and drawbacks. Thereafter, we contrast the strengths and weaknesses of contemporary approaches – i.e., subliminal and preconscious methods – with those of instrumental hypnosis. Showcasing findings using hypnosis, we sketch out how this top-down approach provides the experimental means to foster new perspectives to study the unconscious mind.

PART I – MODERN CONCEPTIONS OF THE UNCONSCIOUS MIND AND THE GLOBAL WORKSPACE THEORY OF CONSCIOUSNESS

Subliminal and preconscious approaches represent active areas of research within the domain of unconscious cognition (Kim and Blake, 2005; Kouider and Dehaene, 2007; Jensen et al., 2011). Guided by various techniques designed to eliminate conscious access of sensory events (Kim and Blake, 2005), subliminal research gave way to the emergence of different theories (Hassin et al., 2005). Critically, conceptions of the unconscious mind remain largely contingent on current theories of consciousness: engaging unconscious perception entails disrupting at least one mechanism that would otherwise enable conscious perception (Dehaene et al., 2006; Kanai et al., 2010; Dehaene, 2011; Dehaene and Changeux, 2011). In the global workspace theory of consciousness, the progression from unconsciousness to consciousness proceeds from the coordinated interplay between multiple local systems forming an overarching network. More specifically, this model posits that conscious perception stems from the bottom-up propagation of sensory signals across various systems, while top-down processes boost the strength of these signals, enabling global broadcast of information through a virtual forum (Baars, 1988, 2005; Dehaene et al., 1998, 2001, 2003, 2006; Dehaene and Naccache, 2001; Dehaene and Changeux, 2005, 2011; Del Cul et al., 2007; Dehaene, 2011). Therefore, according to this account, consciousness corresponds to a stable state that emerges from the coherent and synchronous activities among distant local processing systems.

The global workspace model entails that unconscious processing of sensory events occurs in two ways: conscious suppression of sensory signals, corresponding to perceptual failures, and preconscious processing of sensory events reflecting attentional failures (see **Figure 1**; Dehaene et al., 2006; Kanai et al., 2010; Dehaene and Changeux, 2011). During suppression, interruptions of the sensory signal can potentially occur at different stages of sensory processing, leading to subliminal processing. For example, backward masking – a common suppression technique – likely achieves suppression of consciousness by interfering with local boosting processes of sensory signals, which reduces its overall efficiency for global broadcast (Kouider and Dehaene, 2007). During preconscious processing, various techniques divert attention and top-down amplification processes away from sensory events, thereby preventing global broadcast of information and conscious perception. Several experiments report that individuals remain unaware of unattended events (Simons and Levin, 1997; Mack and Rock, 1998; Simons, 2000). Apart from providing significant information about the influences of subliminal and preconscious processing on cognitions and behaviors, both approaches show that understanding the inner workings of the unconscious mind may echo our views on consciousness. Here we unravel the merits and drawbacks of suppression and inattention techniques through the lens of the global workspace model while putting forward the idea that hypnosis may contribute and extend the range of experimental possibilities to study conscious suppression and the unconscious mind.

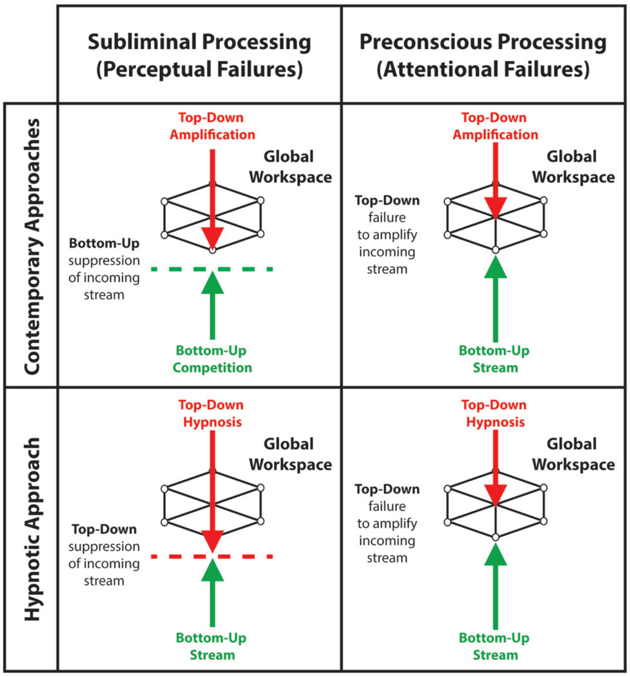


FIGURE 1 | Contemporary approaches and the hypnotic approach as a function of the taxonomy that differentiates subliminal processing, reflecting perceptual failures, from preconscious processing, reflecting attentional failures. During *subliminal processing*: contemporary approaches utilize bottom-up competition between sensory inputs to exploit the limits of perception, prevent global broadcast of incoming signals and induce conscious suppression; while the hypnotic approach harness top-down processes to modulate lower perceptual processes and suppress sensory inputs. During *preconscious processing*: both contemporary approaches and the hypnotic approach prevent global broadcast by hindering top-down amplification of incoming sensory signals.

PART II – CONTEMPORARY APPROACHES TO THE STUDY OF THE COGNITIVE UNCONSCIOUS

SUBLIMINAL SUPPRESSION TECHNIQUES – PERCEPTUAL FAILURES

Interocular suppression techniques

Interocular suppression refers to an assortment of psychophysical techniques that induce conscious suppression of sensory input through the simultaneous dichoptic presentation of dissimilar stimuli (see **Figure 2**). In this procedure, both stimuli compete to access consciousness, resulting in the temporary conscious suppression of the ineffective stimulus (Blake, 2001; Blake and Logothetis, 2002; Lin and He, 2009; Blake et al., 2014).

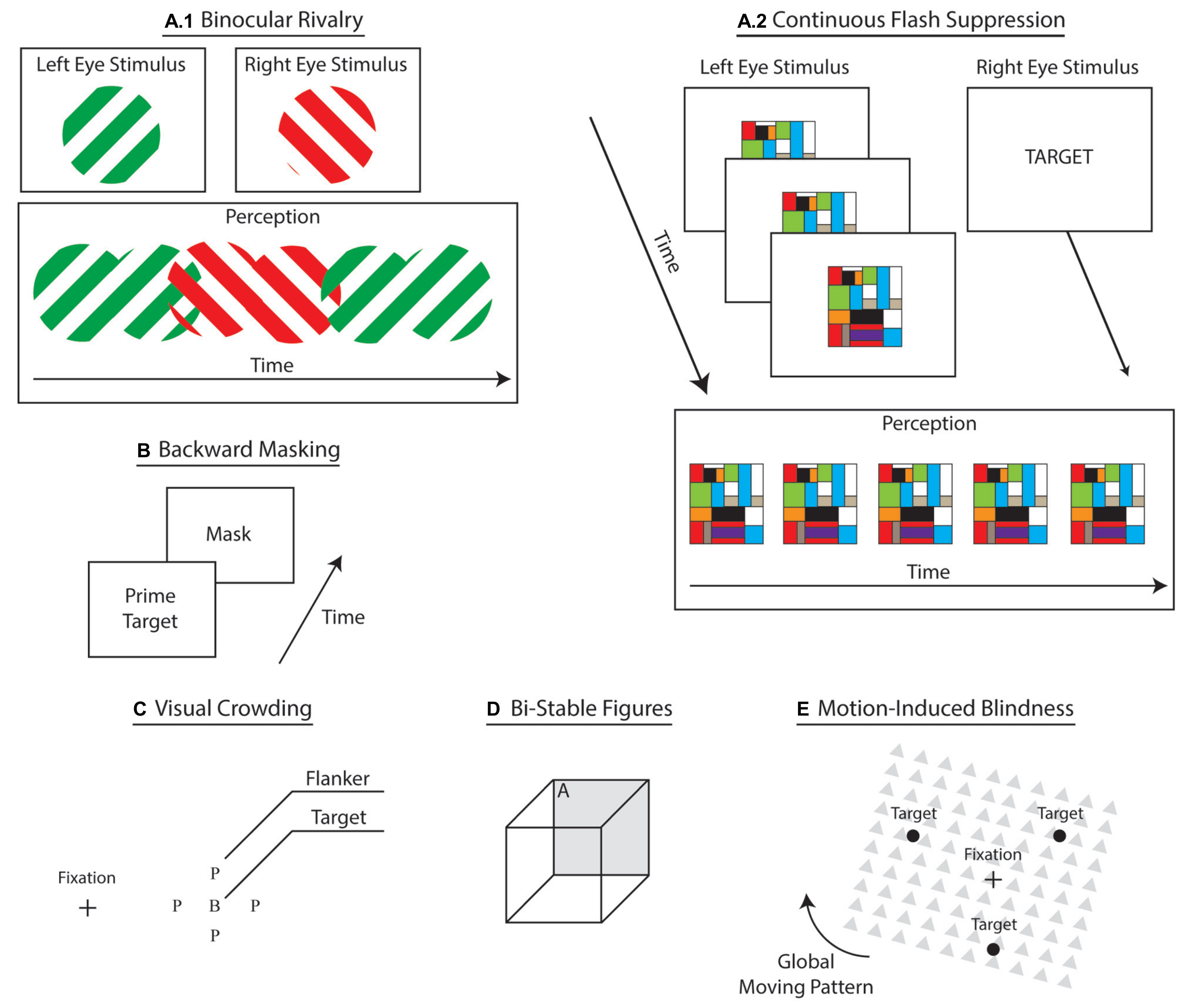


FIGURE 2 | Subliminal techniques. A sketch of the prevailing techniques used to suppress conscious perception of sensory inputs. **(A1)** Binocular rivalry where dichoptic presentation of dissimilar stimuli generates fluctuation in conscious perception between representations. **(A2)** Continuous flash suppression where presentation a repeatedly flashed stimulus to one eye induces conscious suppression of static stimulus presented in the other eye.**(B)** Backward masking where rapid sequential presentation of a prime and a mask conscious induces conscious suppression of the prime. **(C)** Visual crowding where flankers interfere with processing of the target in peripheral vision, rendering certain target-related characteristics unrecognizable. **(D)** Bistable figures induce perceptual fluctuations between mutually exclusive visual interpretations – e.g., side A facing upward and then facing downward. **(E)** Motion-induced blindness where movement of the global pattern suppresses conscious perception of the targets.

During binocular rivalry (BR), participants experience transient, yet unpredictable, switches between perceptions of each monocular stimulus. Flash suppression (Wolfe, 1984) and continuous flash suppression (CFS; Tsuchiya and Koch, 2005) techniques aid to overcome this particular shortcoming by governing stimulus onset, thus controlling perceptual dominance and visual awareness. During CFS, experimenters repeatedly flash a single monocular stimulus – i.e., typically high contrast Mondrian patterns – to induce steadier perceptual dominance (See **Figure 2**), which elicits longer and deeper suppression compared to BR (Tsuchiya et al., 2006). Evidence suggests that adaptation represents a central mechanism of perceptual suppression (Kang and Blake, 2010). Some propose that greater suppression during CFS follows from the reduction of neural adaptation (Tsuchiya et al., 2006; Yang and Blake, 2012). However, it remains unclear whether CFS merely represents a form of BR (Tsuchiya et al., 2006; Shimaoka and Kaneko, 2011). Plus, a recent review of BR casts doubts concerning the potential of this technique to provide researchers with critical information about consciousness (Blake et al., 2014). This review underscores concerns related to the validity of control conditions for BR, the distinction between attention and awareness during BR, the generalizability of findings with BR, and the comparison between the neural correlates of BR and the neural correlates of consciousness (NCC). Indeed, according to the authors, instead of indicating the neural mechanisms involved in awareness, multistable techniques – and ensuing transient perceptual changes – could be highlighting perceptual decision processes. In accordance with this criticism, CFS has widely gained in popularity (cf., this *Frontiers in Psychology* research topic on conscious suppression). Importantly, interocular suppression techniques yield competition at the sensory level and at the representational level (Sterzer et al., 2009b), presumably reflecting corresponding changes a the neural level (Sterzer et al., 2014). Accordingly, most accounts explain interocular suppression of consciousness through inhibitory competition at different levels of processing – i.e., lower-level sensory signal and higher-level representations (Tong et al., 2006). This family of techniques provides the critical advantage of inducing suppression under constant visual input, a methodological feature that permits more reliable comparisons of conscious and unconscious perception without confounding variables related to changes in sensory events.

Backward masking

A popular suppression approach, visual backward masking eliminates conscious access through rapid sequential presentations of stimuli – a prime target and a mask – that result in the conscious suppression of the prime target (see **Figure 2**; Breitmeyer, 2007; Kouider and Dehaene, 2007). Subliminal processing of masked primes show perceptual, cognitive, and ideomotor effects (Breitmeyer and Ögmen, 2006). A dominant view on backward masking proposes that the mask stimulus suppresses conscious access by interfering with local re-entrant signals that boost sensory signals (Breitmeyer, 2007). Thus, by interrupting this boosting process, masking weakens the sensory signal, rendering it impotent for global broadcast and conscious perception (Dehaene et al., 2006; Dehaene and Changeux, 2011). Critically masking reliably interrupts conscious access to sensory signals, yet suppression remains sensitive to various prime-related and experimental-related factors, such as the type of task, novelty of the prime, category of the prime, etc. (Van den Bussche et al., 2009b). Despite advantageous experimental qualities such as flexibility, generalizability, and robustness, backward masking achieves conscious suppression through the disruption of the visual input – i.e., mask interference. This drawback precludes direct contrast between the conscious and unconscious conditions, which differ in sensory processing, thereby limiting our ability to tease apart the NCC with this approach.

Visual crowding

In peripheral vision, nearby distractors – e.g., flankers – render targets unrecognizable (see **Figure 2**; Cavanagh, 2001; Levi, 2008; Whitney and Levi, 2011). This crowding phenomenon aids in uncovering the underlying mechanisms of conscious recognition and object identification (Levi, 2008; Whitney and Levi, 2011). Critically, crowding rarely abolishes conscious access to sensory inputs because target detection remains largely unaffected (Pelli et al., 2004). Instead, crowding capitalizes on the poor resolution of peripheral vision combined with competing noise – e.g., from the flankers – to make the features of the target less discernible (Nandy and Tjan, 2007). The lack of complete suppression of awareness highlights the difficulty in separating subliminal perception from consciousness (Kim and Blake, 2005). Also, similar to backward masking, visual crowding elicits suppression of consciousness through variations of sensory input – i.e., by adding flankers – which further limits our ability to isolate the NCC. Different theories currently compete to explain the effects of visual crowding. According to one such account, the suppression of certain target features proceeds from multilevel interactions comprising a bottleneck situated between lower level features detection and higher order integration processes (Parkes et al., 2001; Levi, 2008; Whitney and Levi, 2011). Supporting this view, the effect of this bottleneck at the integration level shows that targets can systematically acquire certain distractor-related features (Greenwood et al., 2010). These findings suggest a central tendency of the visual system to search for greater consistency under visual constraints, such as those imposed by peripheral vision (Balas et al., 2009; Greenwood et al., 2009; Dakin et al., 2010). In this fashion, instead of combining imprecise information to form an inadequate visual representation, the visual system converges toward a more coherent representation by subtracting uneven information. In line with this multilevel account, previous studies have found distractor-related effects for both elementary features and whole object representations (Whitney and Levi, 2011). These accounts deem unlikely that this bottleneck acts upon a single and unique stage of visual processing (Levi, 2008).

Bistable figures

Bistable figures – e.g., Necker Cube and duck–rabbit figure – are ambiguous images that induce involuntary fluctuations between mutually exclusive interpretations. For example, staring at the Necker Cube leads to sequential changes between two perceptual views – i.e., the frontal face either oriented downward or upward (see **Figure 2**). Bistable representations reflect the inherent ambiguity conveyed by these images as our brain processes resolve these competing interpretations (Leopold and Logothetis, 1999; Kornmeier and Bach, 2012; Ishizu, 2013). Similar to interocular suppression, these figures elicit changes in visual awareness while keeping the sensory input constant. Moreover, because bistable interpretations are mutually exclusive, the perceptual dominance of one interpretation over the other leads to the complete suppression of the other one, giving researchers effective means to investigate subliminal perception. Despite its effectiveness in eliminating conscious perception, an overarching shortcoming permeates this approach: the perceptual switches triggered by ambiguous figures are scantily under the complete voluntary control of participants, reducing experimental control (Kornmeier and Bach, 2006).

It remains uncertain whether perceptual switches hinge on bottom-up or top-down mechanisms (Rach and Huster, 2014). Recognizing evidence favoring both views, hybrid accounts attempt to bridge effects related to bottom-up sensory processing, such as adaptation and fatigue, with top-down higher order processing, like anticipatory and learning factors (Long and Toppino, 2004; Toppino and Long, 2005). Specifically, the relative inability for individuals to exert total control over perceptual switches reflects bottom-up processing, whereas the capacity for observers to intentionally influence these switches demonstrates the effect of top-down processing. This view therefore emphasizes that perceptual switches stem from multilevel interactions between both lower sensory (e.g., Long et al., 1992) and higher cognitive processing (Raz et al., 2007; Knapen et al., 2011; Weilnhammer et al., 2013).

Motion-induced blindness

In motion-induced blindness, salient visual stimuli surrounded by global moving patterns intermittently vanish from visual awareness when participants stare at one location and covertly attend to the disappearing stimuli (see **Figure 2**; Bonneh et al., 2001). Similar to interocular suppression and bistable perception, the high experimental value of this approach largely rests on its ability to fully suppress conscious perception while keeping the sensory input constant (Scholvinck and Rees, 2009). Suppression of conscious perception through such means remains largely unpredictable as multiple factors modulate the effect (e.g., Kawabe et al., 2007; Scholvinck and Rees, 2009). Evidence suggests that suppression of perception under motion-induced blindness is unlikely to result in the pinpointing of a circumscribed brain locus (Donner et al., 2013). Supporting a multilevel account, various mechanisms have been investigated – e.g., adaptation and persistent inhibition (Gorea and Caetta, 2009), motion streak suppression (Wallis and Arnold, 2009), perceptual fill-in (Hsu et al., 2006), or depth perception ordering and surface completion (Graf et al., 2002). At the neural level, corresponding fluctuation of brain activity suggests that variations in conscious perception originate from the on-going competition between the ventral and dorsal pathways, which engage in recognition and spatial processing, respectively (Donner et al., 2008). These fluctuations appear to proceed from the competition between processing of the static targets and of the moving mask.

The depth of subliminal processing

Subliminal perception shows that the enduring influence of suppressed stimuli spans multiple levels of processing, including the perceptual, lexical, semantic and social. Different subliminal approaches reveal that suppression hardly affects superficial level of visual processing, such as spatial frequency, motion-direction, color, and orienting (Long and Toppino, 2004; Breitmeyer and Ögmen, 2006; Breitmeyer, 2007; Whitney and Levi, 2011; Yang and Blake, 2012; Kramer et al., 2013). A more complex picture has emerged concerning deeper levels of subliminal processing (van Gaal and Lamme, 2012). Shaping our views concerning the cognitive unconscious, subliminal processing occurs both at the cortical and subcortical level (Naccache et al., 2005). However, inconsistencies across tasks uncover task-specific differences (e.g., Faivre et al., 2012, 2014; Fogelson et al., 2014; Izatt et al., 2014). Moreover, certain discrepancies within task suggest that task-related and stimuli-related factors influence the depth of subliminal processing (e.g., CFS, Costello et al., 2009; Kang et al., 2011). We should therefore avoid to immediately reconsider the notion that certain subliminal approaches do not engage unconscious semantic processing (Gayet et al., 2014). Yet, various findings indicate that the brain subliminally processes semantic information (Costello et al., 2009; Van den Bussche et al., 2009a; Yeh et al., 2012; Sanguinetti et al., 2013). Likewise, evidence also indicates subliminal processing of faces and affective facial expressions (Jiang et al., 2007; Henson et al., 2008; Kouider et al., 2009; Sterzer et al., 2009a; Adams et al., 2010; Faivre et al., 2012; Doi and Shinohara, 2013; Izatt et al., 2014). Overall, suppression techniques have propelled a research trajectory that encompasses a large body of results. These findings indicate that unconscious processing cuts across multiple cognitive systems, emphasizing the critical role of unconscious processing. Therefore, the variety of suppression techniques often proves useful despite certain limitations.

PRECONSCIOUS SUPPRESSION TECHNIQUES – FAILURES OF ATTENTION

Inattentional blindness and change blindness

Unattended, salient but unexpected events may go unnoticed (Simons and Chabris, 1999; Simons, 2000). Coined *inattentional blindness* (IB), these failures to detect prominent task-irrelevant stimuli occur when individuals engage in a demanding cognitive task (Mack and Rock, 1998). Similarly, inattentive observers can stay unaware of important changes in visual scenes, a phenomenon called *change blindness* (CB; Simons and Levin, 1997). The effects of IB primarily stem from orienting attention toward task-relevant events, preventing perceptual awareness of unattended events (Simons, 2000). Previous studies outline that several factors mediate the effects of IB, including the visual saliency and spatial location of ignored events (e.g., Koivisto et al., 2004), expectations and attentional set of the observer (e.g., Most, 2013), the difficulty of the primary-task and individual expertise (Memmert, 2006; Cartwright-Finch and Lavie, 2007), as well as inhibitory mechanisms near the fringe of the *attentional spotlight* (Thakral and Slotnick, 2010). CB, on the other hand, largely rests on interactions between attention, perception and visual short-term memory (Simons and Rensink, 2005).

Inattentional blindness (IB) and CB mainly reflect lapses of attention, wherein unattended signals lack the necessary energy and sustainability to reach conscious perception (Dehaene et al., 2006; Dehaene, 2011; Dehaene and Changeux, 2011). Both experimental techniques therefore rely on attentional failures instead of suppressive means (Kanai et al., 2010). Supporting this account, neurophysiological studies report that change detection correlates with modulation of the N2pc, an electrophysiological marker of selective attention (Eimer, 1996; Robitaille and Jolicoeur, 2006; Kiss et al., 2008; Mazza et al., 2009; Woodman et al., 2009); whereas the absence of modulation of the N2pc relates to CB (Eimer and Mazza, 2005; Busch et al., 2009; however, see Schankin and Wascher, 2007). Together, these results imply that the top-down amplification processes of selective attention prompt conscious perception of changes in the display. Conversely, in the absence of these amplification processes, sensory inputs of changes remain largely unconscious. In line with these reports, brain imaging studies of CB reveal decreased frontoparietal activity (Beck et al., 2001), a cortical network often linked with attentional processing (Corbetta et al., 2008). In addition, temporary disruption of the right parietal cortex with repetitive transcranial magnetic stimulation (rTMS) significantly impairs change detection abilities and increases CB (Beck et al., 2006; Tseng et al., 2010). Alongside attentional processing, the parietal region also associates with visual short-term memory (Berryhill and Olson, 2008). While the relationship between attention and conscious perception remains difficult to construe (van Boxtel et al., 2010; Tallon-Baudry, 2011; Chica et al., 2013), empirical findings with IB and CB techniques strongly hint that top-down amplification processes play a central role in becoming aware of sensory events.

Unattended events during IB and CB induce preconscious processing, yielding priming effects (e.g., Silverman and Mack, 2006), implicit processing of spatial information (Lathrop et al., 2011) and aversive stimuli (Wiemer et al., 2013), or tacitly influencing decision processes (Laloyaux et al., 2008). Markedly, unattended events during IB and CB induce frontal activity, suggesting deep processing despite inattention (Pessoa and Ungerleider, 2004; Thakral, 2011). However, neurophysiological results of preconscious processing remain ambiguous: whereas some studies report a fronto-central positive deflection indexing preconscious processing of unattended events (Fernandez-Duque et al., 2003; Kimura et al., 2008), results from other studies hardly show any electrophysiological component specific to preconscious processing during CB (Fernandez-Duque et al., 2003; Eimer and Mazza, 2005; Henderson and Orbach, 2006; Pourtois et al., 2006). Several task-related shortcomings limit the application of IB and CB (Kim and Blake, 2005). Importantly, once a participant learns or suspect that the display may contain otherwise covert task-irrelevant stimuli, it largely reduces the likelihood of IB and CB (Jensen et al., 2011). This issue proves particularly challenging for IB when researchers probe participants about the detection of covert events, immediately hinting the presence of concealed elements and invalidating repeated testing (Kim and Blake, 2005). This concern reduces the overall number of trials available. However, despite this liability, both IB and CB apply to a vast range of stimuli. Furthermore, these techniques possess great ecological validity, as failure to attend and detect conspicuous events reproduces outside the laboratory (e.g., Simons and Levin, 1998).

Attentional blink

In a stream of rapidly presented visual stimuli, attending to a task-related stimulus impairs attentional processing of subsequent stimuli at short latencies (Raymond et al., 1992). This attentional blink (AB) leads to a marked decrease in performance that underscores the limit of attentional processing and often leaves participants unaware of unattended stimuli (Shapiro et al., 1997b). Converging evidence suggest that AB largely reflects limitations of attentional capacity (for review, see Martens and Wyble, 2010). Deployed attentional resources toward the primary target temporally impede ensuing attentional processing of incoming sensory signal (Dux and Marois, 2009). Supporting this view, evidence show that greater resources devoted toward processing of the first target increase the magnitude of the AB (Arnell et al., 2007). Contrary to IB and CB, expectations hardly modulate AB, making it a highly reliable experimental design (Kim and Blake, 2005). Deep processing of non-reported targets accompanies AB. For example, unattended words facilitate ensuing processing of semantically related words (Shapiro et al., 1997a; Martens et al., 2002). Neurophysiological results also indicate that non-reported items yield modulations of the N400, an electrophysiological component indexing semantic processing (Luck et al., 1996; Rolke et al., 2001; however, see Batterink et al., 2010). However, evidence suggests that enduring preconscious processing of semantics during AB remains contingent to task demands (Giesbrecht et al., 2007). Neuroimaging results of AB indicate that unattended stimuli activate occipitotemporal regions in the near-absence of frontal activity (Marois et al., 2004; Kranczioch et al., 2005; Marti et al., 2012). In addition, brain injury to the parietal region increases the AB (Husain et al., 1997; Shapiro et al., 2002). Despite the robustness of the AB effects, this methodological paradigm relies on variation of stimuli and temporal constraints. Moreover, since these effects occur within a narrow and precise time window, researchers can hardly test them outside the laboratory. Overall, the AB represents a reliable task to investigate the underlying top-down mechanisms gating access to conscious perception in a tightly controlled fashion (e.g., Sergent et al., 2005).

HYPNOSIS AS AN ADJUNCT TO SUBLIMINAL AND PRECONSCIOUS APPROACHES

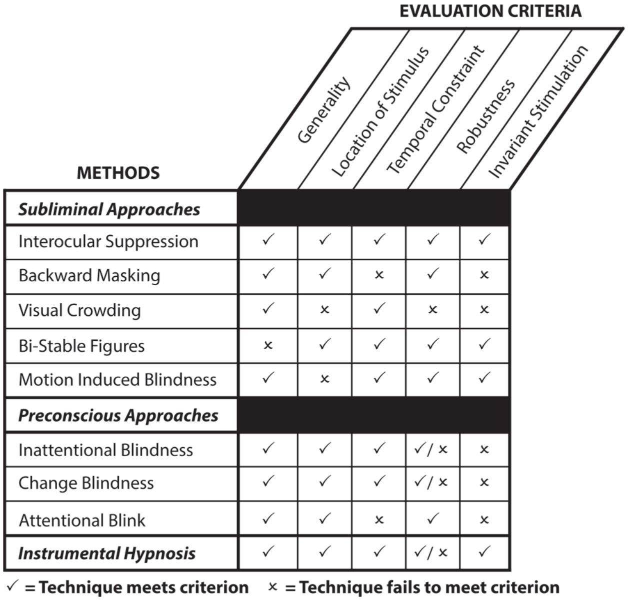
Subliminal approaches exploit the limits of perception to suppress awareness of sensory events (Dehaene et al., 2006; Kanai et al., 2010; Dehaene and Changeux, 2011). These techniques mainly utilize competition between perceptual processing of sensory signals or representations to induce unawareness, wherein the dominance of a sensory signal or a representation prompts the suppression of subdominant ones (Blake and Logothetis, 2002). Importantly, while attentional processing moderates subliminal processing (Naccache et al., 2002; Kiefer and Brendel, 2006; Kiefer and Martens, 2010; Martens et al., 2011), conscious suppression hardly involves top-down factors. Instead, the effects of subliminal processing stem from weakened sensory signals and subdominant perceptual representations. Accordingly, subliminal approaches hinge on perceptual failures. Conversely, preconscious approaches rests on the disruption of top-down amplification processes, thereby preventing conscious access to sensory events (Naccache et al., 2002; Dehaene et al., 2006; Kanai et al., 2010). As a result, this approach may involve the processing of sensory signals strong enough for global broadcast, yet these signals remain incapable of surpassing the threshold of consciousness without the necessary top-down amplification (Dehaene et al., 2006). In this way, preconscious processing reflects attentional failures. The distinction between subliminal and preconscious approaches represents a reliable taxonomy of unconscious processing based on the differences between perceptual and attentional failures (**Figure 1**; Kanai et al., 2010).

The broad range of mechanisms selectively engaged by each of the abovementioned methods challenges our capacity to generalize findings across different tasks. As we explained, these techniques yield important findings about the scope and depth of subliminal and preconscious processing. Notably, bottom-up approaches afford researchers with plentiful experimental control, yet offer limited ecological validity. Conversely, top-down approaches, such as IB and CB, propose an ecological tactic to investigate unconscious processing (Simons and Levin, 1997; Simons, 2000; Simons and Rensink, 2005; Jensen et al., 2011), but remain experimentally challenged by top-down factors. For example, the popular invisible gorilla paradigm represents a compelling framework that generalizes to everyday tasks (Simons and Chabris, 1999), yet suffers from limited empirical control and methodological practicality (Kim and Blake, 2005). These key observations shape the trajectory of current research on subliminal and preconscious research. Moreover, they raise important empirical and theoretical questions about our ability to bridge the gap between these different methods. Here we submit that instrumental hypnosis – a top-down approach, which relies on higher cognitive functions regulating the downstream operations of the perceptual and affective systems – offers new investigative prospects to elucidate the unconscious mind. Moreover we argue that this unique approach transcends the subliminal versus preconscious taxonomy, as hypnosis can induce perceptual and attentional failures. Overall, hypnosis provides the means to replicate established findings and explore new hypotheses.

To assess the aforementioned techniques (see **Figure 3**), we follow the criteria put forth in the literature (Kim and Blake, 2005). This set of criteria evaluates the efficacy of each technique and gauges the potential of experimental methods to generate reliable and valid findings concerning unconscious processes:

(i) *Generality*: whether the technique applies to a broad range of stimuli or only to a select few.

(ii) *Stimulus location*: whether the stimulus has to be presented at the center or the periphery of the visual field.



METHODS	EVALUATION CRITERIA				
	Generality	Location of Stimulus	Temporal Constraint	Robustness	Invariant Stimulation
Subliminal Approaches					
Interocular Suppression	✓	✓	✓	✓	✓
Backward Masking	✓	✓	×	✓	×
Visual Crowding	✓	×	✓	×	×
Bi-Stable Figures	×	✓	✓	✓	✓
Motion Induced Blindness	✓	×	✓	✓	✓
Preconscious Approaches					
Inattentional Blindness	✓	✓	✓	✓/×	×
Change Blindness	✓	✓	✓	✓/×	×
Attentional Blink	✓	✓	×	✓	×
Instrumental Hypnosis	✓	✓	✓	✓/×	✓

✓ = Technique meets criterion × = Technique fails to meet criterion

FIGURE 3 | Strengths and weaknesses of contemporary techniques to investigate unconscious perception and instrumental hypnosis as a function of evaluation criteria. *Generality*: whether the technique applies to a broad range of stimuli or only to a selected few. *Location of stimulus*: whether the stimulus has to be presented at the center or the periphery of the visual field to induce conscious suppression or inattention. *Temporal constraint*: whether the technique imposes a temporal constraint relative to the duration of the stimulus presentation. *Robustness*: whether the technique completely abolishes awareness. *Invariant stimulation*: whether conscious suppression requires significant modifications of sensory events to make a stimulus invisible. A "✓" indicates that the technique meets this particular criterion, whereas an "×" indicates that the technique fails to meet this particular criterion.

(iii) *Temporal constraint*: whether the technique imposes a temporal constraint relative to the duration of the stimulus presentation.

(iv) *Robustness*: whether this technique completely abolishes awareness.

(v) *Invariant stimulation*: whether conscious suppression requires significant modifications of sensory events to make a stimulus invisible – e.g., adding a mask to induce conscious suppression during backward masking.

PART III – USING HYPNOSIS TO INVESTIGATE THE UNCONSCIOUS MIND

HYPNOSIS: A TOP-DOWN APPROACH TO INVESTIGATE THE UNCONSCIOUS MIND

Hypnosis represents an increasingly popular area of research in cognitive science, including notable ventures in the domains of perception, attention, memory, and motor control (Nash and Barnier, 2008). For example, hypnotic suggestions represent central vehicles in exploring the notion of automatic processing and induce de-automatization of ballistic responses in the Stroop, McGurk, and Simon effects (Raz et al., 2002, 2005; Iani et al., 2006; Lifshitz et al., 2013; Déry et al., 2014). Within this growing field of research, scholars and clinicians conceptualize the scientific investigation of hypnosis in a dichotomous fashion, differentiating intrinsic research on hypnosis, which focuses on the phenomenon itself, from an instrumental approach, where researchers employ hypnosis as an experimental tool to investigate cognition (Oakley and Halligan, 2009, 2013). Our view focuses on supplementing current experimental methodologies with this instrumental strategy to further unravel the cognitive unconscious.

Theoretical frameworks for hypnosis largely cluster around the appellations of state and non-state models. State theories posit that hypnosis implies a particular psychological state – e.g., an altered state of consciousness – whereas non-state theories typically argue that hypnosis essentially reduces to sociocognitive factors such as motivation and compliance (Kirsch and Lynn, 1995; Kallio and Revonsuo, 2003; Kirsch, 2011; Raz, 2011a; Mazzoni et al., 2013). In spite of this conceptual distinction, the use of hypnosis often includes an induction phase to increase mental absorption followed by a suggestion phase providing directions to elicit particular changes in thoughts and behaviors. Hypnotic responses usually result from hypnotic suggestions. The degree of responsiveness to hypnotic suggestions represents a robust measure with normal distribution and high test-retest reliability (Piccione et al., 1989). Highly hypnotically suggestible individuals (HHSs), as opposed to low hypnotically suggestible individuals (LHSs), characteristically respond to "cognitive" suggestions – i.e., suggestions that involve changes in perception and memory (Kirsch et al., 1999). Accordingly, researchers often compare the performances of HHSs and LHSs to demonstrate the effects of hypnosis (Nash and Barnier, 2008).

Top-down regulatory processes – e.g., attention, cognitive control and monitoring – play a central role in mediating responses to hypnotic suggestions (Crawford, 1994; Gruzelier, 1998; Raz, 2004, 2011b; Egner and Raz, 2007; Dienes, 2012; Lifshitz et al., 2012; Dienes and Hutton, 2013). Specifically, hypnosis modulates top-down processes to dramatically change the implementation of cognitive strategies during hypnotic responses (Egner and Raz, 2007). Furthermore, the execution of hypnotic responses often appears dissociated from voluntary control, as they generally feel involuntary and effortless (Spanos et al., 1977). This phenomenological aspect represents a critical component of hypnotic phenomena (Kirsch and Lynn, 1998). A family of prevalent theories contends that this central property of hypnosis mainly reflects decoupling between cognitive control and monitoring processes (cf., Jamieson and Woody, 2007; Woody and Sadler, 2008). According to this view, hypnosis not only alters cognitive control but also modifies the supervision of these control processes. Supporting this view, a neuroimaging study of HHSs report a functional disconnection between the lateral prefrontal cortex, often linked to cognitive control processes, and the anterior cingulate cortex (ACC), a brain region associated with cognitive monitoring (Egner et al., 2005). This finding echoes numerous brain imagining studies of hypnosis that show similar modulations of the ACC in the absence of specific hypnotic suggestion (Faymonville et al., 2000, 2003; Rainville et al., 2002; McGeown et al., 2009; Vanhaudenhuyse et al., 2009; Deeley et al., 2012; Müller et al., 2012, 2013).

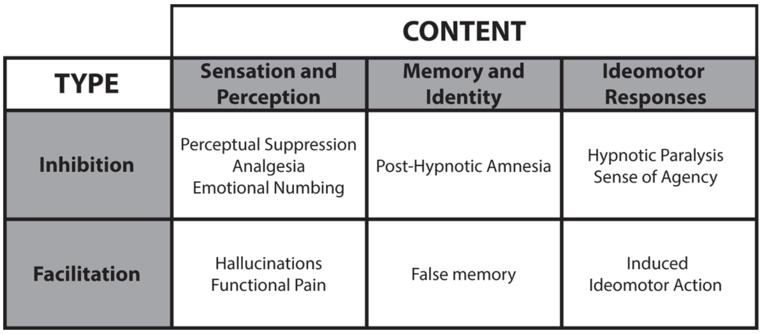
Emphasizing the importance of individual variability, compliant participants frequently report using different cognitive strategies to successfully respond to the very same suggestion (McConkey et al., 1989; Heap et al., 2004). This inter-individual variability in hypnotic responses raises questions concerning the link between specific cognitive styles and hypnotic susceptibility, which hints that specific sub-types of cognitive profiles could enable greater hypnotic responses (Terhune et al., 2011; Brown and Oakley, 2004). In this respect, some scholars argue that what characterizes HHSs is their greater cognitive flexibility (Crawford, 1994; Gruzelier, 1998); others regard the improvement in attention and inhibitory control as a near-universal outcome (Dienes et al., 2009; Varga et al., 2011). Supporting the cognitive flexibility view, neuroimaging findings from HHSs show increased functional connectivity between the dorsolateral prefrontal cortex (DLPFC), a cortical region strongly associated with cognitive control, and saliency networks, which likely mediate somatic, automatic, and emotional information (Hoeft et al., 2012). However, a recent study report that temporary disruption of the DLPFC with rTMS also causes modifications of hypnotic responses, hinting that hypnosis could reflect the disruption of cognitive control and monitoring (Dienes and Hutton, 2013). Resting-state brain imaging studies show that HHSs show decreased activity in the anterior part of default mode network (DMN), a brain network negatively correlated with goal-directed activity (McGeown et al., 2009). Reduced activity in the anterior part of DMN may therefore indicate a propensity to engage in goal-driven behaviors – i.e., the mental preparation to comply with hypnotic suggestions and produce hypnotic responses. Other studies also report a significant change in DMN activity related to hypnosis (Demertzi et al., 2011; Deeley et al., 2012; Lipari et al., 2012). Taken together, these cumulative findings intimate the importance of top-down regulatory functions in hypnotic phenomena.

HYPNOSIS AS A VEHICLE TO UNCOVER THE UNCONSCIOUS MIND

Hypnotic suggestions divide as a function of type and content (see **Figure 4**; Woody and Sadler, 2008). Within this framework, suggestions either facilitate or suppress cognitions and behaviors. For example, facilitation may yield hallucinations (e.g., Bryant and Mallard, 2003), whereas suppression can interfere with consciousness (e.g., Bryant and Kourch, 2001). Accordingly, researchers can test conscious and unconscious processing in a fully orthogonal manner (see **Figure 5**), a significant experimental benefit to better isolate the NCC. The content of hypnotic suggestions selectively targets specific mental functions and behaviors. Thus, we will demonstrate how hypnosis encompasses a wide variety of experimental possibilities to investigate unconscious processes (Oakley and Halligan, 2009, 2013; Cox and Barnier, 2010; Bortolotti et al., 2012). Importantly, because hypnotic suggestions can either induce suppression of consciousness or influence attentional processing to impede top-down amplification, this top-down approach bridge the subliminal versus preconscious dichotomy (see **Figure 1**). Here we discuss several avenues based on such research developments.

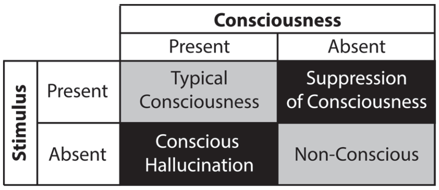
Sensation and perception

Hypnosis selectively targets and modifies perception of sensory events. For example, it can alter perception of colors (Kosslyn et al., 2000; Mallard and Bryant, 2001; Spiegel, 2003; McGeown et al., 2009; Kallio and Koivisto, 2013; Koivisto et al., 2013), induce compelling experiences of grapheme-color synesthesia – a condition characterized by perceptual experiences of anomalous



	CONTENT		
TYPE	Sensation and Perception	Memory and Identity	Ideomotor Responses
Inhibition	Perceptual Suppression Analgesia Emotional Numbing	Post-Hypnotic Amnesia	Hypnotic Paralysis Sense of Agency
Facilitation	Hallucinations Functional Pain	False memory	Induced Ideomotor Action

FIGURE 4 | Hypnotic suggestions divide as a function of type and content. These various hypnotic suggestions yield numerous hypnotic effects.



		Consciousness	
		Present	Absent
Stimulus	Present	Typical Consciousness	Suppression of Consciousness
	Absent	Conscious Hallucination	Non-Conscious

FIGURE 5 | Balanced experimental design using instrumental hypnosis where contrast between conscious suppression – i.e., stimulus is present and consciousness is absent – and conscious hallucination – i.e., stimulus is absent and consciousness is present – enable targeting of neural correlates of consciousness.

combinations of cross-modal sensations (Cohen Kadosh et al., 2009; however, see Anderson et al., 2014), and even temporarily abolish co-occurrences of secondary sensory experiences in synesthetes (Terhune et al., 2010).[1] Indicating the reliability and sustainability of these remarkable changes, hypnotically induced alteration of color perception correlates with corresponding modifications in neural response (Kosslyn et al., 2000; McGeown et al., 2012). Specifically, neuroimaging results of hypnotically induced altered perception show modulation of brain regions associated with color processing – i.e., bilateral fusiform gyrus, primary visual area (Kosslyn et al., 2000; McGeown et al., 2012). Importantly, this phenomenon raises intriguing questions regarding the study of subliminal processing, because such changes in perception entail the suppression from consciousness of the actual sensory event. For example, would suppressing green sensory input by supplanting it with hypnotically induced hallucinations produce green-related priming effects? The affirmative would support the subliminal processing of hypnotically induced suppressed content. Such questions bear on the investigation of top-down-induced subliminal processing. Recent neurophysiological investigations found that alteration of color perception correlates with modulations of neural oscillatory activity over posterior regions (Koivisto et al., 2013). These modulations of neuronal responses submit the idea of an early mechanism involved in probing the stored mental representation of the suggested color and in the modification of the ensuing percept. Consistent with the idea that hypnotic suggestions to alter color perception operate preconsciously, participants barely detect perceptual or sensory changes, suggesting that these alterations precede conscious access (Kallio and Koivisto, 2013). Suppression of sensory signals arguably precedes the global broadcast. Supporting this early top-down effect on sensory input, event-related potentials indicate hypnotic modulations of primary visual components (i.e., P1 and N1; Raz et al., 2005).

Hypnosis also modulates phenomenological aspects of conscious experience, such as pain perception (Patterson and Jensen, 2003; Jensen and Patterson, 2006; Price and Rainville, 2013). Called hypnotic analgesia, this phenomenon does not follow from the release of endogenous analgesics (Goldstein and Hilgard, 1975) or an increased state of relaxation (Miller et al., 1991). Instead, hypnotic analgesia arguably originates from various factors, including the alteration of expectations relative to impending painful events, as well as attentional and emotional regulation mechanisms (Kiernan et al., 1995; Rainville et al., 1999a; Ploghaus et al., 2003; Koyama et al., 2005; Price and Rainville, 2013). Hypnotic analgesia triggers pain-related inhibitory neural mechanisms (Vanhaudenhuyse et al., 2009). Similar to color perception, these changes in perception demonstrate how hypnosis elicits powerful effects over perceptual experience. Brain imaging studies of this phenomenon underline a dissociation between the somatosensory cortex, involved in processing of nociceptive signals, and the ACC, a region associated with conscious access to pain sensation (Rainville et al., 1997, 1999b, 2002; Faymonville et al., 2000, 2003; Hofbauer et al., 2001). Grounded in this functional dissociation between sensory and affective components of pain (Rainville et al., 1999a), current findings suggest that alteration of pain perception can either proceed from direct interferences of sensory processing (Hofbauer et al., 2001), akin to subliminal approaches, or by modulating conscious access to pain sensation (Rainville et al., 2002), comparable to preconscious approaches. In line with this view, neurophysiological results imply that hypnotic analgesia affects early as well as late stages of nociceptive processing (De Pascalis et al., 2008). Analogous to the color-hallucination paradigm, such changes in pain perception raise important questions concerning the effects of unconscious nociceptive processing on behavior. For example, would unconscious processing of nociceptive stimuli still instigate a level of discomfort? Moreover, in addition to analgesia, hypnotic suggestions can also trigger functional pain – i.e., the subjective experience of pain in the absence of a noxious stimulus (Derbyshire et al., 2004). This functional aspect of hypnosis brings about the experimental ability to compare, in a balanced design, conscious perception in the absence of a stimulus and the lack of conscious perception in the presence of a stimulus, in order to effectively isolate the NCC (see **Figure 5**).

Memory and identity

Posthypnotic amnesia (PHA) represents memory lapses of events that took place under hypnosis, after termination of hypnotic induction (Kihlstrom, 1985, 1997; Barnier, 2002a). Affording researchers with increased experimental control, these memory deficits contributed to the development of experimental research on implicit cognition (Barnier et al., 2001). Importantly, prearranged post-hypnotic cues induce recall, implying that memory lapses mainly reflect the inability to access and retrieve stored information rather than encoding and storage deficits (Geiselman et al., 1983; Kihlstrom, 1997). Hence, PHA putatively originates from top-down failures to access and retrieve information, relating this phenomenon to preconscious approaches. The underlying neurophysiological correlates of PHA involve the modulations of attentional processes relative to access and selection of stored information (Allen et al., 1995; Schnyer and Allen, 1995). In addition, compared to normal retrieval of stored information, PHA correlates with decreased activity in the extrastriate and temporal cortical regions, as well as increased activity in the rostral lateral PFC (Mendelsohn et al., 2008). This reduced activity in the temporal lobes likely reflects the incapacity to successful access

---

[1] Hypnotically induced blindness could represent another case of conscious suppression, however the phenomenological status of these phenomena remains rather ambiguous (Oakley and Halligan, 2009).

stored information, as this brain region strongly associates with long-term memory storage (Wixted and Squire, 2011). Hypothetically, increased PFC activity could reflect the implementation of hypnotic responses to actively hinder retrieval processes.

Past research shows that temporarily irretrievable material influences behavior nonetheless (Kihlstrom, 1980; Spanos et al., 1982; Kinnunen and Zamansky, 1996; Bryant et al., 1999; Barnier et al., 2001). For example, reflecting the distinction between explicit and implicit memory systems, performances of HHSs on a word association task denote PHA-related priming effects despite significant deficits on explicit recall (Kihlstrom, 1980; David et al., 2000; Barnier et al., 2001). PHA experiments also reveal suppression of conscious access to episodic memory (Kihlstrom, 1997), source memory (Evans and Kihlstrom, 1973; Evans, 1979), and even autobiographical memory (Barnier and McConkey, 1999; Barnier, 2002a,b; Cox and Barnier, 2003; Barnier et al., 2004). Notably, suppression of access to autobiographical memories may lead to significant effects on personal identity (Barnier, 2002b). These examples illustrate how PHA offers a unique framework to test various hypotheses on the cognitive unconscious beyond perceptual processing.

Contrary to PHA, few studies looked at the effects of hypnotic agnosia – i.e., the functional inability to access semantic knowledge (Kihlstrom, 1997; Raz, 2011b). This research gap leaves open numerous experimental possibilities to probe unconscious semantic processing using hypnosis, stretching from the semantic categories of inaccessible items to modality specific deficits. Furthermore, the case of hypnotic agnosia evokes an intriguing paradox wherein the selective interference to access a particular semantic content requires the ability to minimally identify that content at some level – e.g., the hypnotically induced discriminating inability to recognize scissors, requires the tacit ability to discriminate scissors from other objects. This phenomenon therefore demonstrates how top-down processing may act through tacit knowledge – i.e., knowledge in the absence of awareness.

Ideomotor response

Hypnosis can decouple volitions and actions (Halligan et al., 2000; Blakemore et al., 2003; Ward et al., 2003; Cojan et al., 2009; Cardeña et al., 2012; Coutlee and Huettel, 2012; Peter et al., 2012; Deeley et al., 2013a,b, 2014; however, see Haggard et al., 2004). Hypnotic suggestions directly targeted at the sense of control disrupt willed actions and induce alien control. For example, during involuntary arm levitation, responsive participants raise their arm in the absence of conscious control (Blakemore et al., 2003). This hypnotic effect reduces overall muscle activity (Peter et al., 2012) and relates to significant changes in the cerebellar-parietal network (Blakemore et al., 2003). These results parallel brain-imaging studies that report modulation of parietal activation during hypnotically induced paralysis, wherein participants experience the inability to move a limb (Cojan et al., 2009; Cardeña et al., 2012; Coutlee and Huettel, 2012; Deeley et al., 2013a). Investigating the effects of hypnotic suggestion on the perception of voluntary and involuntary movements, a recent neuroimaging study reports that loss of perceived control correlates with decreased connectivity between the supplementary motor area, associated with motor planning, and the primary motor area (Deeley et al., 2013a). These results suggest that decoupling the planning and the implementation of actions decreases the feeling of control during movements. Additional results from this study also indicate that reduced conscious perception of involuntary actions correlates with decrease neural activity of the parietal lobe, suggesting that modulation of parietal activity relates more strongly with awareness of movements than feeling of control. In a separate study, the same research group investigated involuntary movements as a function of locus of control (Deeley et al., 2014). Results show that induced involuntary control may reflect various types of alien control and modulations of agency. Thus, various strategies may interfere with conscious access to feelings of control. Together, these findings highlight how ideomotor suggestions elicit important interactions between hypnotic response, awareness of movement and locus of control. Moreover, they also show how conscious access to the control of movements influences the phenomenology of action.

Thought suppression and hypnotically induced clinical analogs

Intrusive cognitions and emotions often accompany psychopathology (Wenzlaff and Wegner, 2000). In order to aid patients, clinicians use hypnosis to suppress unwanted thoughts (Bryant and Wimalaweera, 2006; Bryant and Sindicich, 2007). Moreover, hypnotic suggestions can also numb the conscious perception of unpleasant emotions (Bryant and Kourch, 2001; Bryant and Mallard, 2002; Bryant, 2005; Bryant and Kapur, 2006; Bryant and Fearns, 2007; Sebastiani et al., 2007). Experimental results show that hypnotic numbing of emotions significantly reduces emotional and somatic responses to aversive stimuli (Bryant and Kourch, 2001; Bryant and Mallard, 2002). Furthermore, emphasizing the accuracy of hypnotic suggestions, evidence also indicates that emotional suppression solely interferes with affective dimensions of cognition, leaving the cognitive content available for conscious processing (Bryant and Fearns, 2007). Interestingly, an experimental study investigated the interactions between masked-induced and hypnotically induced suppression mechanisms. Using a backward masking design, results show that hypnotically induced emotional numbing suppresses subliminal processing of masked aversive stimuli, thereby demonstrating that hypnotic suppression of emotions occurs at the unconscious level – i.e., prior to global broadcast (Bryant, 2005). Hence, hypnotic suppression acts early and can supersede subliminal processing. Together, hypnotic suppression of thoughts and emotions provide a reliable and distinctive framework to investigate subliminal processing.

In experimental psychopathology, hypnotic suggestions target specific functions and dramatically influence cognitions and behaviors (Oakley, 2006; Cox and Barnier, 2010; Woody and Szechtman, 2011; Bortolotti et al., 2012). For example, one study used hypnosis to interfere with subjective feelings associated with task completion and motivational security, producing obsessive-compulsive-like behaviors in typical participants (Woody et al., 2005). This study underlines the importance of conscious access to certain affective signals in the phenomenology of even the utmost mundane tasks – e.g., washing your hands. In the same vein, hypnosis can also eliminate conscious access to selfhood-related information, yielding mirrored-self misidentification delusions –

a monothematic delusion characterized by the inability to recognize self-reflections in the mirror (Barnier et al., 2010; Connors et al., 2012a,b, 2013). Evidence shows that this induced delusion stems from faces recognition impairment (Connors et al., 2012a, 2013). Critically, hypnotically induced mirror agnosia – i.e., unavailability of knowledge about mirrors – also facilitates the generation of mirrored-self misidentification analogs (Connors et al., 2012b). Aside from exploring new hypotheses, research with hypnotically induced clinical analogs underlines the importance of conscious access to various sources of information, such as sense of completion or selfhood-related recognition. From this perspective, conscious suppression not only provides critical information about the unconscious mind, but also helps to identify the functional role of various processes related to consciousness by looking at hypnotically induced maladapted behaviors and delusions.

The fields of neuropsychology and behavioral neurology often feature deficits that are amenable to top-down influences (Weiskrantz, 1986; Cowey, 2010; Overgaard, 2011) at different levels (Marshall and Halligan, 1995; Fink et al., 1996). Experimental accounts of hypnosis show how hypnotic suggestions can induce reversible neuropsychological conditions – a form of behavioral analog to TMS (cf., Raz and Wolfson, 2010). One example is visuospatial hemineglect, where hypnotic suggestions to favor one visual hemifield over the other lead to significant decreases in visual performance on the neglected side and neglect-like symptoms (Oakley and Halligan, 2009, see supplementary material; Raz, 2004; Priftis et al., 2011). In accordance with neuropsychological findings that show distinctive levels of unconscious processing, e.g., evidence from visuospatial neglect reveals processing of coarse global representation in the absence awareness (Marshall and Halligan, 1995), hypnotically induced neglect can reliably expand this line of research. Similar to prevailing preconscious approaches, this research strategy underlines the experimental potential of hypnosis to foster critical information about the link between orienting of attention and visual awareness, and opens novel avenues to investigate the preconscious processing of unattended stimuli.

The experimental potential of hypnosis

Whether hypnosis acts through suppressive means or influences attention to impede conscious access, this top-down methodological approach possesses formidable potential to study the unconscious mind. Two general features make hypnosis a unique approach. First, hypnotic suggestions afford researchers with a wide spectrum of experimental possibilities. Second, whereas the prevailing approaches either take advantage of perceptual limitations or interfere with top-down amplification processes, hypnosis harness top-down processes to investigate both subliminal and preconscious phenomena. Indeed, due to the variety of hypnotic suggestions, hypnosis can prompt perceptual and attentional failures. Also, the accuracy of hypnosis (Raz and Michels, 2007) allows researchers to selectively target mechanisms gating access to consciousness.

As illustrated previously, hypnotic phenomena comprise numerous brain systems, depending on the content of the hypnotic suggestion and the targeted function. Therefore hypnotic suggestions act through various means: while certain suggestions engage suppression mechanisms and yield subliminal processing, other suggestions interfere with the deployment of top-down amplification and elicit preconscious processing (see **Figure 1**). During hypnotically induced subliminal and preconscious processing, hypnotic responses recruit frontal networks implicated in top-down attentional regulation, control and monitoring processes (Rainville et al., 1999b; Casale et al., 2012; Kihlstrom, 2013; Oakley and Halligan, 2013). As mentioned previously, these brain regions associate with the implementation of cognitive strategies to successfully comply with hypnotic suggestions. Subsequent neural effects putatively reflect the targeted function of the hypnotic suggestion (Oakley, 2008). For example, alterations of colour perception correspond with significant changes in the visual areas (Kosslyn et al., 2000; McGeown et al., 2012) and oscillatory modulations of posterior brain activity 70 to 120 milliseconds post stimulus onset (Koivisto et al., 2013). These results suggest the presence of an early mechanism that supplants the actual representation of sensory events with the suggestion-related stored representation, subsequently producing alteration of perception and suppressing sensory input. In addition, because hypnosis supposedly elicits modifications of monitoring processes, perceptual alterations could also involve modifications of reality monitoring – i.e., the cognitive ability to assess the authenticity of changes in perception (Bryant and Mallard, 2003, 2005). Contemporary subliminal approaches and hypnotic approach therefore encompass different suppression mechanisms. Whereas the former exploits perceptual limitations, the latter use top-down mechanisms to suppress conscious perception. Conversely, hypnotically induced preconscious processing resembles prevailing preconscious approaches. For example, hypnotic responses can also orient attention away from sensory events, thereby impeding top-down amplification of sensory signals (Raz, 2004; Oakley and Halligan, 2009; Priftis et al., 2011). In addition, heightened mental absorption during hypnosis (Rainville et al., 2002) could tax attentional resources, triggering similar effects to the AB. In summary, the hypnotic approach to elucidate unconscious processing rests on a broad variety of mechanisms. This wide spectrum offers various experimental possibilities that overlap both subliminal and preconscious processing.

Overall, the use of hypnosis to investigate the cognitive unconscious compares favorably to contemporary methodologies (see **Figure 3**): this approach applies to a broad range of visual and non-visual stimuli; works equally well for stimuli presented centrally or peripherally; hardly necessitates temporal constraint relative to the presentation of the stimulus or variation in sensory events. Finally, various experiments imply the robustness of unconscious hypnotic phenomena, even if the phenomenological dimensions of hypnosis remain roughly defined (Rainville and Price, 2003; Jamieson, 2007). This approach also offer the following advantages: first, because it yields subliminal or preconscious processing while keeping sensory inputs constant, this technique provides researchers with greater experimental validity to isolate conscious from unconscious processing. As mentioned previously, this feature invites direct comparisons between conscious processing and unconscious processing without introducing confounding variables relative to changes in the sensory input. Second, hypnosis may selectively suppress certain content from conscious experience – e.g., emotions – without altering the whole perceptual experience. This methodological benefit becomes particularly useful in the context of concurrent presentations of sensory events. In addition, hypnosis may harness the ecological benefits of preconscious approaches. Finally, this approach may also be used in conjunction with other suppression methods; a feature that expands the methodological possibilities through the various combinations it creates. Exemplifying this malleability, HHSs exhibit distinctive response patterns to masked primes (Bryant, 2005). In comparisons to other techniques, hypnosis therefore represents a valid and reliable instrument to probe the unconscious mind.

Despite these benefits, certain obstacles to the use of hypnosis in the context of the suppression of consciousness might arise. Here we address some of these concerns. First, HHSs are often carefully selected in hypnosis experiments to demonstrate the full potential of hypnotic suggestions (Hilgard, 1965), despite constituting only 10 to 15% of the population. This situation entails that interpretations of such experiments might not generalize and could merely reflect certain psychological characteristics of this particular group of individuals. A similar concern pertains to the fact that certain scholars consider hypnosis as a specific form of altered consciousness, which suggests that the effects of hypnosis might reduce to this specific altered mental state, again hindering generalizability. However, the notion that hypnosis implies a particular mental state remains highly debatable (Kirsch and Lynn, 1995; Kirsch, 2011). More importantly, both objections fail to apply to the instrumental approach, wherein hypnosis serves as an experimental tool to investigate cognition, and do not focus on hypnosis by itself. In the instrumental context, psychometric specificities of hypnosis are typically disregarded because they hardly provide insight into the model or hypothesis being tested. For example, the application of instrumental hypnosis to investigate the notion of automaticity proposes novel perspectives about this central psychological construct regardless of psychometric characteristics of hypnosis (Raz et al., 2002, 2005; Iani et al., 2006; Campbell et al., 2012; Lifshitz et al., 2013). For this reason, questions about generalizability are mostly irrelevant. A third concern follows from inter-individual variability in hypnotic responses, an epistemological obstacle that highlights the heterogeneous nature of responsiveness. Despite the importance of taking this aspect into consideration, this variability among individuals only calls for precautions when it comes to interpreting the data. In addition, qualitative data could properly assess and control for this variability. Indeed, a growing array of interviewing techniques, such as the elicitation interview, provide tools for identifying cognitive strategies (Vermersch, 1994; Le Van Quyen and Petitmengin, 2002).

A final concern pertains to the objective control of subjects' awareness, a central issue that transcends research on conscious and unconscious processes (Seth et al., 2008; Overgaard and Timmermans, 2010). Alongside subjective reports, the subliminal and preconscious approaches typically control for conscious perception by ensuring that unconscious-related performances remain at chance level (Kouider and Dehaene, 2007). These performance-based strategies, however, often miscalculate conscious perception because subjective reports may vary while objective measures stay constant (Lau and Passingham, 2006). Optimally, research involving hypnosis requires two fundamental contrasts: hypnotic versus non-hypnotic experimental conditions, as well as HHSs versus LHSs. These comparisons provide the means to properly screen for, measure the effects of, and thereby bolster the effects of hypnotic suggestions (Mazzoni et al., 2013). Subsequently, two pivotal strategies likely enable better control of awareness. First, researchers may use concomitant objective measures to the primary task. For example, during emotional numbing, somatic measures corroborate emotional suppression (Bryant and Mallard, 2002). However, this strategy largely assumes that concomitant objective measures represent a tight control for subjective experience – an unwarranted assumption. Because they rarely represent an infallible control of awareness (Sandberg et al., 2010), concomitant objective measures only propose convergent evidence. Second, researchers may control for hypnotic effects using a secondary task; for example, Stroop (MacLeod, 1991) or color-based digit detection (Cohen Kadosh et al., 2009) may control for alterations of color perception. In the absence of robust control strategies, converging evidence from multiple measures represents the best strategy to remedy this lacuna (Seth et al., 2008).

CONCLUSION

Here we herald instrumental hypnosis as a new experimental vehicle to probe the structure and functioning of the cognitive unconscious. Whereas most current techniques investigate the unconscious mind via subliminal approaches that challenge our perceptual limitations and preconscious approaches that rest on inattention, the hypnosis lens facilitates both suppression and inattention via top-down mechanisms. Beyond the empirical potential to explore novel ideas and hypotheses, top-down control provides scientists with increased experimental flexibility by allowing target processing of specific sensory events. Moreover, hypnotic hallucinations provide an efficient means to capture the NCC using a full two-by-two balanced design allowing for a direct comparison of conscious and unconscious conditions. Thus, scholars stand to benefit from the use of hypnosis in their quest to better understand the underpinnings of the unconscious mind (Raz, 2011b). Incorporating this tool into the armamentarium available to investigators of the cognitive unconscious will likely pave the road to a more encompassing scientific understanding of this budding field.

ACKNOWLEDGMENTS

Mathieu Landry acknowledges support from Fonds de Recherche du Québec – Nature et Technologies. Dr. Amir Raz acknowledges support from the Canada Research Chair program, the Canadian Institutes of Health Research, the Natural Sciences and Engineering Research Council of Canada, and the Fonds de Recherche du Québec – Santé.

REFERENCES

Adams, W. J., Gray, K. L. H., Garner, M., and Graf, E. W. (2010). High-level face adaptation without awareness. *Psychol. Sci.* 21, 205–210. doi: 10.1177/0956797609359508

Allen, J. J., Iacono, W. G., Laravuso, J. J., and Dunn, L. A. (1995). An event-related potential investigation of posthypnotic recognition amnesia. *J. Abnorm. Psychol.* 104, 421–430. doi: 10.1037/0021-843X.104.3.421

Anderson, H. P., Seth, A. K., Dienes, Z., and Ward, J. (2014). Can grapheme-color synesthesia be induced by hypnosis? *Front. Hum. Neurosci.* 8:220. doi: 10.3389/fnhum.2014.00220

Arnell, K. M., Killman, K. V., and Fijavz, D. (2007). Blinded by emotion: target misses follow attention capture by arousing distractors in RSVP. *Emotion* 7, 465–477. doi: 10.1037/1528-3542.7.3.465

Baars, B. J. (1988). *A Cognitive Theory of Consciousness.* Cambridge: Cambridge University Press.

Baars, B. J. (2005). Global workspace theory of consciousness: toward a cognitive neuroscience of human experience. *Prog. Brain Res.* 150, 45–53. doi: 10.1016/S0079-6123(05)50004-9

Bachner-Melman, R., and Lichtenberg, P. (2001). Freud's relevance to hypnosis: a reevaluation. *Am. J. Clin. Hypn.* 44, 37–50. doi: 10.1080/00029157.2001.10403454

Balas, B., Nakano, L., and Rosenholtz, R. (2009). A summary-statistic representation in peripheral vision explains visual crowding. *J. Vis.* 9, 13.1–13.18 doi: 10.1167/9.12.13

Barnier, A. J. (2002a). Posthypnotic amnesia for autobiographical episodes: a laboratory model of functional amnesia? *Psychol. Sci.* 13, 232–237. doi: 10.1111/1467-9280.00443

Barnier, A. J. (2002b). Remembering and forgetting autobiographical events: instrumental uses of hypnosis. *Contemp. Hypn.* 19, 51–61. doi: 10.1002/ch.242

Barnier, A. J., Bryant, R. A., and Briscoe, S. (2001). Posthypnotic amnesia for material learned before or during hypnosis: explicit and implicit memory effects. *Int. J. Clin. Exp. Hypn.* 49, 286–304. doi: 10.1080/00207140108410079

Barnier, A. J., Cox, R. E., Connors, M. H., Langdon, R., and Coltheart, M. (2010). A stranger in the looking glass: developing and challenging a hypnotic mirrored-self misidentification delusion. *Int. J. Clin. Exp. Hypn.* 59, 1–26. doi: 10.1080/00207144.2011.522863

Barnier, A. J., and McConkey, K. M. (1999). Autobiographical remembering and forgetting: what can hypnosis tell us? *Int. J. Clin. Exp. Hypn.* 47, 346–365. doi: 10.1080/00207149908410041

Barnier, A. J., McConkey, K. M., and Wright, J. (2004). Posthypnotic amnesia for autobiographical episodes: influencing memory accessibility and quality. *Int. J. Clin. Exp. Hypn.* 52, 260–279. doi: 10.1080/0020714049052351

Batterink, L., Karns, C. M., Yamada, Y., and Neville, H. (2010). The role of awareness in semantic and syntactic processing: an ERP attentional blink study. *J. Cogn. Neurosci.* 22, 2514–2529. doi: 10.1162/jocn.2009.21361

Beck, D. M., Muggleton, N. G., Walsh, V., and Lavie, N. (2006). Right parietal cortex plays a critical role in change blindness. *Cereb. Cortex* 16, 712–717. doi: 10.1093/cercor/bhj017

Beck, D. M., Rees, G., Frith, C. D., and Lavie, N. (2001). Neural correlates of change detection and change blindness. *Nat. Neurosci.* 4, 645–650. doi: 10.1038/88477

Berryhill, M. E., and Olson, I. R. (2008). The right parietal lobe is critical for visual working memory. *Neuropsychologia* 46, 1767–1774. doi: 10.1016/j.neuropsychologia.2008.01.009

Blake, R. (2001). A primer on binocular rivalry, including current controversies. *Brain Mind* 2, 5–38. doi: 10.1023/A:1017925416289

Blake, R., Brascamp, J., and Heeger, D. J. (2014). Can binocular rivalry reveal neural correlates of consciousness? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 369, 1471–2970.

Blake, R., and Logothetis, N. (2002). Visual competition. *Nat. Rev. Neurosci.* 3, 13–21. doi: 10.1038/nrn701

Blakemore, S. J., Oakley, D. A., and Frith, C. D. (2003). Delusions of alien control in the normal brain. *Neuropsychologia* 41, 1058–1067. doi: 10.1016/S0028-3932(02)00313-5

Bonneh, Y. S., Cooperman, A., and Sagi, D. (2001). Motion-induced blindness in normal observers. *Nature* 411, 798–801. doi: 10.1038/35081073

Bortolotti, L., Cox, R. E., and Barnier, A. J. (2012). Can we recreate delusions in the laboratory? *Philos. Psychol.* 25, 109–131. doi: 10.1080/09515089.2011.569909

Breitmeyer, B. G. (2007). Visual masking: past accomplishments, present status, future developments. *Adv. Cogn. Psychol.* 3, 9–20. doi: 10.2478/v10053-008-0010-7

Breitmeyer, B. G., and Ögmen, H. (2006). *Visual Masking: Time Slices Through Conscious and Unconscious Vision*, Vol. 41. New York: Oxford University Press. doi: 10.1093/acprof:oso/9780198530671.001.0001

Brown, R. J., and Oakley, D. A. (2004). "An integrative cognitive theory of hypnosis and high hypnotizability," in *High Hypnotizability: Theoretical, Experimental and Clinical Perspectives*, eds R. J. Brown and D. A. Oakley (New York: Bruner-Routledge), 152–186.

Bryant, R. A. (2005). Hypnotic emotional numbing: a study of implicit emotion. *Int. J. Clin. Exp. Hypn.* 53, 26–36. doi: 10.1080/00207140490914225

Bryant, R. A., Barnier, A. J., Mallard, D., and Tibbits, R. (1999). Posthypnotic amnesia for material learned before hypnosis. *Int. J. Clin. Exp. Hypn.* 47, 46–64. doi: 10.1080/00207149908410022

Bryant, R. A., and Fearns, S. (2007). Taking the feeling out of emotional memories – a study of hypnotic emotional numbing: a brief communication. *Int. J. Clin. Exp. Hypn.* 55, 426–434. doi: 10.1080/00207140701506508

Bryant, R. A., and Kapur, A. (2006). Hypnotically induced emotional numbing: the roles of hypnosis and hypnotizability. *Int. J. Clin. Exp. Hypn.* 54, 281–291. doi: 10.1080/00207140600689462

Bryant, R. A., and Kourch, M. (2001). Hypnotically induced emotional numbing. *Int. J. Clin. Exp. Hypn.* 49, 220–230. doi: 10.1080/00207140108410072

Bryant, R. A., and Mallard, D. (2002). Hypnotically induced emotional numbing: a real-simulating analysis. *J. Abnorm. Psychol.* 111, 203–207. doi: 10.1037/0021-843X.111.1.203

Bryant, R. A., and Mallard, D. (2003). Seeing is believing: The reality of hypnotic hallucinations. *Conscious. Cogn.* 12, 219–230. doi: 10.1016/S1053-8100(03)00003-5

Bryant, R. A., and Mallard, D. (2005). Reality monitoring in hypnosis: a real-simulating analysis. *Int. J. Clin. Exp. Hypn.* 53, 13–25. doi: 10.1080/00207140490914216

Bryant, R. A., and Sindicich, N. (2007). Hypnosis and thought suppression – more data: a brief communication. *Int. J. Clin. Exp. Hypn.* 56, 37–46. doi: 10.1080/00207140701672995

Bryant, R. A., and Wimalaweera, S. (2006). Enhancing thought suppression with hypnosis. *Int. J. Clin. Exp. Hypn.* 54, 488–499. doi: 10.1080/00207140600857002

Busch, N. A., Fründ, I., and Herrmann, C. S. (2009). Electrophysiological evidence for different types of change detection and change blindness. *J. Cogn. Neurosci.* 22, 1852–1869. doi: 10.1162/jocn.2009.21294

Campbell, N. K., Blinderman, I. M., Lifshitz, M., and Raz, A. (2012). Converging evidence for de-automatization as a function of suggestion. *Conscious. Cogn.* 21, 1579–1581. doi: 10.1016/j.concog.2012.05.007

Cardeña, E., Lehmann, D., Faber, P. L., Jönsson, P., Milz, P., Pascual-Marqui, R. D., et al. (2012). EEG sLORETA functional imaging during hypnotic arm levitation and voluntary arm lifting. *Int. J. Clin. Exp. Hypn.* 60, 31–53. doi: 10.1080/00207144.2011.622184

Cartwright-Finch, U., and Lavie, N. (2007). The role of perceptual load in inattentional blindness. *Cognition* 102, 321–340. doi: 10.1016/j.cognition.2006.01.002

Casale, A. D., Ferracuti, S., Rapinesi, C., Serata, D., Sani, G., Savoja, V., et al. (2012). Neurocognition under hypnosis: findings from recent functional neuroimaging studies. *Int. J. Clin. Exp. Hypn.* 60, 286–317. doi: 10.1080/00207144.2012.675295

Cavanagh, P. (2001). Seeing the forest but not the trees. *Nat. Neurosci.* 4, 673–674. doi: 10.1038/89436

Chica, A. B., Paz-Alonso, P. M., Valero-Cabré, A., and Bartolomeo, P. (2013). Neural bases of the interactions between spatial attention and conscious perception. *Cereb. Cortex* 23, 1269–1279. doi: 10.1093/cercor/bhs087

Cohen Kadosh, R., Henik, A., Catena, A., Walsh, V., and Fuentes, L. J. (2009). Induced cross-modal synaesthetic experience without abnormal neuronal connections. *Psychol. Sci.* 20, 258–265. doi: 10.1111/j.1467-9280.2009.02286.x

Cojan, Y., Waber, L., Schwartz, S., Rossier, L., Forster, A., and Vuilleumier, P. (2009). The brain under self-control: modulation of inhibitory and monitoring cortical networks during hypnotic paralysis. *Neuron* 62, 862–875. doi: 10.1016/j.neuron.2009.05.021

Connors, M. H., Barnier, A. J., Coltheart, M., Cox, R. E., and Langdon, R. (2012a). Mirrored-self misidentification in the hypnosis laboratory: recreating the delusion from its component factors. *Cogn. Neuropsychiatry* 17, 151–176. doi: 10.1080/13546805.2011.582287

Connors, M. H., Cox, R. E., Barnier, A. J., Langdon, R., and Coltheart, M. (2012b). Mirror agnosia and the mirrored-self misidentification delusion: a hypnotic analogue. *Cogn. Neuropsychiatry* 17, 197–226. doi: 10.1080/13546805.2011.582770

Connors, M. H., Barnier, A. J., Langdon, R., Cox, R. E., Polito, V., and Coltheart, M. (2013). A laboratory analogue of mirrored-self misidentification delusion: the role of hypnosis, suggestion, and demand characteristics. *Conscious. Cogn.* 22, 1510–1522. doi: 10.1016/j.concog.2013.10.006

Corbetta, M., Patel, G., and Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron* 58, 306–324. doi: 10.1016/j.neuron.2008.04.017

Costello, P., Jiang, Y., Baartman, B., McGlennen, K., and He, S. (2009). Semantic and subword priming during binocular suppression. *Conscious. Cogn.* 18, 375–382. doi: 10.1016/j.concog.2009.02.003

Coutlee, C. G., and Huettel, S. A. (2012). The functional neuroanatomy of decision making: prefrontal control of thought and action. *Brain Res.* 1428, 3–12. doi: 10.1016/j.brainres.2011.05.053

Cowey, A. (2010). The blindsight saga. *Exp. Brain Res.* 200, 3–24. doi: 10.1007/s00221-009-1914-2

Cox, R. E., and Barnier, A. J. (2003). Posthypnotic amnesia for a first romantic relationship: forgetting the entire relationship versus forgetting selected events. *Memory* 11, 307–318. doi: 10.1080/09658210244000108

Cox, R. E., and Barnier, A. J. (2010). Hypnotic illusions and clinical delusions: hypnosis as a research method. *Cogn. Neuropsychiatry* 15, 202–232. doi: 10.1080/13546800903319884

Crawford, H. J. (1994). Brain dynamics and hypnosis: attentional and disattentional processes. *Int. J. Clin. Exp. Hypn.* 42, 204–232. doi: 10.1080/00207149408409352

Dakin, S. C., Cass, J., Greenwood, J. A., and Bex, P. J. (2010). Probabilistic, positional averaging predicts object-level crowding effects with letter-like stimuli. *J. Vis.* 10, 14. doi: 10.1167/10.10.14

David, D., Brown, R., Pojoga, C., and David, A. (2000). The impact of posthypnotic amnesia and directed forgetting on implicit and explicit memory: new insights from a modified process dissociation procedure. *Int. J. Clin. Exp. Hypn.* 48, 267–289. doi: 10.1080/00207140008415246

Deeley, Q., Oakley, D. A., Toone, B., Bell, V., Walsh, E., Marquand, A. F., et al. (2013a). The functional anatomy of suggested limb paralysis. *Cortex* 49, 411–422. doi: 10.1016/j.cortex.2012.09.016

Deeley, Q., Walsh, E., Oakley, D. A., Bell, V., Koppel, C., Mehta, M. A., et al. (2013b). Using hypnotic suggestion to model loss of control and awareness of movements: an exploratory fMRI study. *PLoS ONE* 8:e78324. doi: 10.1371/journal.pone.0078324

Deeley, Q., Oakley, D. A., Toone, B., Giampietro, V., Brammer, M. J., Williams, S. C. R., et al. (2012). Modulating the default mode network using hypnosis. *Int. J. Clin. Exp. Hypn.* 60, 206–228. doi: 10.1080/00207144.2012.648070

Deeley, Q., Oakley, D. A., Walsh, E., Bell, V., Mehta, M. A., and Halligan, P. W. (2014). Modelling psychiatric and cultural possession phenomena with suggestion and fMRI. *Cortex* 53, 107–119. doi: 10.1016/j.cortex.2014.01.004

Dehaene, S. (2011). Conscious and nonconscious processes: distinct forms of evidence accumulation? *Biol. Phys.* 60, 141–168. doi: 10.1007/978-3-0346-0428-4_7

Dehaene, S., and Changeux, J. P. (2005). Ongoing spontaneous activity controls access to consciousness: a neuronal model for inattentional blindness. *PLoS Biol.* 3:e141. doi: 10.1371/journal.pbio.0030141

Dehaene, S., and Changeux, J. P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron* 70, 200–227. doi: 10.1016/j.neuron.2011.03.018

Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., and Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn. Sci.* 10, 204–211. doi: 10.1016/j.tics.2006.03.007

Dehaene, S., Kerszberg, M., and Changeux, J. P. (1998). A neuronal model of a global workspace in effortful cognitive tasks. *Proc. Natl. Acad. Sci. U.S.A.* 95, 14529–14534. doi: 10.1073/pnas.95.24.14529

Dehaene, S., and Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition* 79, 1–37. doi: 10.1016/S0010-0277(00)00123-2

Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J.-F., Poline, J.-B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nat. Neurosci.* 4, 752–758. doi: 10.1038/89551

Dehaene, S., Sergent, C., and Changeux, J. P. (2003). A neuronal network model linking subjective reports and objective physiological data during conscious perception. *Proc. Natl. Acad. Sci. U.S.A.* 100, 8520–8525. doi: 10.1073/pnas.1332574100

Del Cul, A., Baillet, S., and Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biol.* 5:e260. doi: 10.1371/journal.pbio.0050260

Demertzi, A., Soddu, A., Faymonville, M. E., Bahri, M. A., Gosseries, O., Vanhaudenhuyse, A., et al. (2011). Hypnotic modulation of resting state fMRI default mode and extrinsic network connectivity. *Prog. Brain Res.* 193, 309–322.

De Pascalis, V., Cacace, I., and Massicolle, F. (2008). Focused analgesia in waking and hypnosis: effects on pain, memory, and somatosensory event-related potentials. *Pain* 134, 197–208. doi: 10.1016/j.pain.2007.09.005

Derbyshire, S. W. G., Whalley, M. G., Stenger, V. A., and Oakley, D. A. (2004). Cerebral activation during hypnotically induced and imagined pain. *Neuroimage* 23, 392–401. doi: 10.1016/j.neuroimage.2004.04.033

Déry, C., Campbell, N. K. J., Lifshitz, M., and Raz, A. (2014). Suggestion overrides automatic audiovisual integration. *Conscious. Cogn.* 24, 33–37. doi: 10.1016/j.concog.2013.12.010

Dienes, Z. (2012). "Is hypnotic responding the strategic relinquishment of metacognition?," in *Foundations of Metacognition*, eds M. Beran, J. L. Brandl, J. Perner, and J. Proust (Oxford: Oxford University Press), 267–277.

Dienes, Z., Brown, E., Hutton, S., Kirsch, I., Mazzoni, G., and Wright, D. B. (2009). Hypnotic suggestibility, cognitive inhibition, and dissociation. *Conscious. Cogn.* 18, 837–847. doi: 10.1016/j.concog.2009.07.009

Dienes, Z., and Hutton, S. (2013). Understanding hypnosis metacognitively: rTMS applied to left DLPFC increases hypnotic suggestibility. *Cortex* 49, 386–392. doi: 10.1016/j.cortex.2012.07.009

Doi, H., and Shinohara, K. (2013). Unconscious Presentation of Fearful Face Modulates Electrophysiological Responses to Emotional Prosody. *Cereb. Cortex* doi: 10.1093/cercor/bht282 [Epub ahead of print].

Donner, T. H., Sagi, D., Bonneh, Y. S., and Heeger, D. J. (2008). Opposite neural signatures of motion-induced blindness in human dorsal and ventral visual cortex. *J. Neurosci.* 28, 10298–10310. doi: 10.1523/JNEUROSCI.2371-08.2008

Donner, T. H., Sagi, D., Bonneh, Y. S., and Heeger, D. J. (2013). Retinotopic patterns of correlated fluctuations in visual cortex reflect the dynamics of spontaneous perceptual suppression. *J. Neurosci.* 33, 2188–2198. doi: 10.1523/JNEUROSCI.3388-12.2013

Dux, P. E., and Marois, R. (2009). The attentional blink: a review of data and theory. *Atten. Percept. Psychophys.* 71, 1683–1700. doi: 10.3758/APP.71.8.1683

Egner, T., Jamieson, G. A., and Gruzelier, J. (2005). Hypnosis decouples cognitive control from conflict monitoring processes of the frontal lobe. *Neuroimage* 27, 969–978. doi: 10.1016/j.neuroimage.2005.05.002

Egner, T., and Raz, A. (2007). "Cognitive control processes and hypnosis," in *Hypnosis and Conscious States*, ed. G. Jamieson (New York: Oxford University Press).

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalogr. Clin. Neurophysiol.* 99, 225–234. doi: 10.1016/0013-4694(96)95711-9

Eimer, M., and Mazza, V. (2005). Electrophysiological correlates of change detection. *Psychophysiology* 42, 328–342. doi: 10.1111/j.1469-8986.2005.00285.x

Evans, F. J. (1979). Contextual forgetting: posthypnotic source amnesia. *J. Abnorm. Psychol.* 88, 556–563. doi: 10.1037/0021-843X.88.5.556

Evans, F. J., and Kihlstrom, J. F. (1973). Posthypnotic amnesia as disrupted retrieval. *J. Abnorm. Psychol.* 82, 317. doi: 10.1037/h0035003

Faivre, N., Berthet, V., and Kouider, S. (2012). Nonconscious influences from emotional faces: a comparison of visual crowding, masking, and continuous flash suppression. *Front. Psychol.* 3:129. doi: 10.3389/fpsyg.2012.00129

Faivre, N., Berthet, V., and Kouider, S. (2014). Sustained invisibility through crowding and continuous flash suppression: a comparative review. *Front. Psychol.* 5:475. doi: 10.3389/fpsyg.2014.00475

Faymonville, M.-E., Laureys, S., Degueldre, C., DelFiore, G., Luxen, A., Franck, G., et al. (2000). Neural mechanisms of antinociceptive effects of hypnosis. *Anesthesiology* 92, 1257–1267. doi: 10.1097/00000542-200005000-00013

Faymonville, M.-E., Roediger, L., Del Fiore, G., Delgueldre, C., Phillips, C., Lamy, M., et al. (2003). Increased cerebral functional connectivity underlying the antinociceptive effects of hypnosis. *Cogn. Brain Res.* 17, 255–262. doi: 10.1016/S0926-6410(03)00113-7

Fernandez-Duque, D., Grossi, G., Thornton, I. M., and Neville, H. J. (2003). Representation of change: separate electrophysiological markers of attention, awareness, and implicit processing. *J. Cogn. Neurosci.* 15, 491–507. doi: 10.1162/089892903321662895

Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S., and Dolan, R. J. (1996). Where in the brain does visual attention select the forest and the trees? *Nature* 382, 626–628. doi: 10.1038/382626a0

Fogelson, S. V., Kohler, P. J., Miller, K. J., Granger, R., and Tse, P. U. (2014). Unconscious neural processing differs with method used to render stimuli invisible. *Front. Psychol.* 5:601. doi: 10.3389/fpsyg.2014.00601

Gayet, S., Van der Stigchel, S., and Paffen, C. L. E. (2014). Breaking continuous flash suppression: competing for consciousness on the pre-semantic battlefield. *Front. Psychol.* 5:460. doi: 10.3389/fpsyg.2014.00460

Geiselman, R. E., Bjork, R. A., and Fishman, D. L. (1983). Disrupted retrieval in directed forgetting: a link with posthypnotic amnesia. *J. Exp. Psychol. Gen.* 112, 58–72. doi: 10.1037/0096-3445.112.1.58

Giesbrecht, B., Sy, J. L., and Elliott, J. C. (2007). Electrophysiological evidence for both perceptual and postperceptual selection during the attentional blink. *J. Cogn. Neurosci.* 19, 2005–2018. doi: 10.1162/jocn.2007.19.12.2005

Goldstein, A., and Hilgard, E. R. (1975). Failure of the opiate antagonist naloxone to modify hypnotic analgesia. *Proc. Natl. Acad. Sci. U.S.A.* 72, 2041–2043. doi: 10.1073/pnas.72.6.2041

Gorea, A., and Caetta, F. (2009). Adaptation and prolonged inhibition as a main cause of motion-induced blindness. *J. Vis.* 9, 16.11–16.17. doi: 10.1167/9.6.16

Graf, E. W., Adams, W. J., and Lages, M. (2002). Modulating motion-induced blindness with depth ordering and surface completion. *Vision Res.* 42, 2731–2735. doi: 10.1016/S0042-6989(02)00390-5

Greenwood, J. A., Bex, P. J., and Dakin, S. C. (2009). Positional averaging explains crowding with letter-like stimuli. *Proc. Natl. Acad. Sci. U.S.A.* 106, 13130–13135. doi: 10.1073/pnas.0901352106

Greenwood, J. A., Bex, P. J., and Dakin, S. C. (2010). Crowding changes appearance. *Curr. Biol.* 20, 496–501. doi: 10.1016/j.cub.2010.01.023

Gruzelier, J. (1998). A working model of the neurophysiology of hypnosis: a review of evidence. *Contemp. Hypn.* 15, 3–21. doi: 10.1002/ch.112

Haggard, P., Cartledge, P., Dafydd, M., and Oakley, D. A. (2004). Anomalous control: when "free-will" is not conscious. *Conscious. Cogn.* 13, 646–654. doi: 10.1016/j.concog.2004.06.001

Halligan, P. W., Athwal, B. S., Oakley, D. A., and Frackowiak, R. S. (2000). Imaging hypnotic paralysis: implications for conversion hysteria. *Lancet* 355, 986–987. doi: 10.1016/S0140-6736(00)99019-6

Hassin, R. R., Uleman, J. S., and Bargh, J. A. (2005). *The New Unconscious.* Oxford: Oxford University Press.

Heap, M., Brown, R. J., and Oakley, D. A. (2004). *The Highly Hypnotizable Person: Theoretical, Experimental and Clinical Issues.* London: Routledge.

Henderson, R. M., and Orbach, H. S. (2006). Is there a mismatch negativity during change blindness? *Neuroreport* 17, 1011–1015. doi: 10.1097/01.wnr.0000223390.36457.b4

Henson, R. N., Mouchlianitis, E., Matthews, W. J., and Kouider, S. (2008). Electrophysiological correlates of masked face priming. *Neuroimage* 40, 884–895. doi: 10.1016/j.neuroimage.2007.12.003

Hilgard, E. R. (1965). *Hypnotic Susceptibility.* Oxford: Harcourt, Brace & World.

Hoeft, F., Gabrieli, J. D., Whitfield-Gabrieli, S., Haas, B. W., Bammer, R., Menon, V., et al. (2012). Functional brain basis of hypnotizability. *Arch. Gen. Psychiatry* 69, 1064–1072. doi: 10.1001/archgenpsychiatry.2011.2190

Hofbauer, R. K., Rainville, P., Duncan, G. H., and Bushnell, M. C. (2001). Cortical representation of the sensory dimension of pain. *J. Neurophysiol.* 86, 402–411.

Hsu, L. C., Yeh, S. L., and Kramer, P. (2006). A common mechanism for perceptual filling-in and motion-induced blindness. *Vision Res.* 46, 1973–1981. doi: 10.1016/j.visres.2005.11.004

Husain, M., Shapiro, K., Martin, J., and Kennard, C. (1997). Abnormal temporal dynamics of visual attention in spatial neglect patients. *Nature* 385, 154–156. doi: 10.1038/385154a0

Iani, C., Ricci, F., Gherri, E., and Rubichi, S. (2006). Hypnotic suggestion modulates cognitive conflict: the case of the flanker compatibility effect. *Psychol. Sci.* 17, 721–727. doi: 10.1111/j.1467-9280.2006.01772.x

Ishizu, T. (2013). Disambiguation of ambiguous figures in the brain. *Front. Hum. Neurosci.* 7:501. doi: 10.3389/fnhum.2013.00501

Izatt, G., Dubois, J., Faivre, N., and Koch, C. (2014). A direct comparison of unconscious face processing under masking and interocular suppression. *Front. Psychol.* 5:659. doi: 10.3389/fpsyg.2014.00659

Jamieson, G. A. (2007). *Hypnosis and Conscious States: The Cognitive Neuroscience Perspective.* New York: Oxford University Press.

Jamieson, G. A., and Woody, E. (2007). "Dissociated control as a paradigm for cognitive neuroscience research and theorizing in hypnosis," in *Hypnosis and Conscious States: The Cognitive Neuroscience Perspective*, ed. G. A. Jamieson (New York, NY: Oxford University Press), 111–132.

Jensen, M. P., and Patterson, D. R. (2006). Hypnotic treatment of chronic pain. *J. Behav. Med.* 29, 95–124. doi: 10.1007/s10865-005-9031-6

Jensen, M. S., Yao, R., Street, W. N., and Simons, D. J. (2011). Change blindness and inattentional blindness. *Wiley Interdiscip. Rev. Cogn. Sci.* 2, 529–546. doi: 10.1002/wcs.130

Jiang, Y., Costello, P., and He, S. (2007). Processing of invisible stimuli: advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychol. Sci.* 18, 349–355. doi: 10.1111/j.1467-9280.2007.01902.x

Kallio, S., and Koivisto, M. (2013). Posthypnotic suggestion alters conscious color perception in an automatic manner. *Int. J. Clin. Exp. Hypn.* 61, 371–387. doi: 10.1080/00207144.2013.810446

Kallio, S., and Revonsuo, A. (2003). Hypnotic phenomena and altered states of consciousness: a multilevel framework of description and explanation. *Contemp. Hypn.* 20, 111–164. doi: 10.1002/ch.273

Kanai, R., Walsh, V., and Tseng, C.-H. (2010). Subjective discriminability of invisibility: a framework for distinguishing perceptual and attentional failures of awareness. *Conscious. Cogn.* 19, 1045–1057. doi: 10.1016/j.concog.2010.06.003

Kang, M.-S., and Blake, R. (2010). What causes alternations in dominance during binocular rivalry? *Atten. Percepti. Psychophys.* 72, 179–186. doi: 10.3758/APP.72.1.179

Kang, M.-S., Blake, R., and Woodman, G. F. (2011). Semantic analysis does not occur in the absence of awareness induced by interocular suppression. *J. Neurosci.* 31, 13535–13545. doi: 10.1523/JNEUROSCI.1691-11.2011

Kawabe, T., Yamada, Y., and Miura, K. (2007). How an abrupt onset cue can release motion-induced blindness. *Conscious. Cogn.* 16, 374–380. doi: 10.1016/j.concog.2006.06.009

Kiefer, M., and Brendel, D. (2006). Attentional modulation of unconscious "automatic" processes: evidence from event-related potentials in a masked priming paradigm. *J. Cogn. Neurosci.* 18, 184–198. doi: 10.1162/jocn.2006.18.2.184

Kiefer, M., and Martens, U. (2010). Attentional sensitization of unconscious cognition: task sets modulate subsequent masked semantic priming. *J. Exp. Psychol. Gen.* 139, 464. doi: 10.1037/a0019561

Kiernan, B. D., Dane, J. R., Phillips, L. H., and Price, D. D. (1995). Hypnotic analgesia reduces R-III nociceptive reflex: further evidence concerning the multifactorial nature of hypnotic analgesia. *Pain* 60, 39–47. doi: 10.1016/0304-3959(94)00134-Z

Kihlstrom, J. F. (1980). Posthypnotic amnesia for recently learned material: interactions with "episodic" and "semantic" memory. *Cogn. Psychol.* 12, 227–251. doi: 10.1016/0010-0285(80)90010-9

Kihlstrom, J. F. (1985). "Posthypnotic amnesia and the dissociation of memory," in *The Psychology of Learning and Motivation*, ed. G. H. Bower (New York: Academic Press), 131–178.

Kihlstrom, J. F. (1987). The cognitive unconscious. *Science* 237, 1445–1452. doi: 10.1126/science.3629249

Kihlstrom, J. F. (1997). Hypnosis, memory and amnesia. *Philos. Trans. R. Soc. B Biol. Sci.* 352, 1727–1732. doi: 10.1098/rstb.1997.0155

Kihlstrom, J. F. (2013). Neuro-hypnotism: prospects for hypnosis and neuroscience. *Cortex* 49, 365–374. doi: 10.1016/j.cortex.2012.05.016

Kim, C. Y., and Blake, R. (2005). Psychophysical magic: rendering the visible "invisible." *Trends Cogn. Sci.* 9, 381–388. doi: 10.1016/j.tics.2005.06.012

Kimura, M., Katayama, J. I., and Ohira, H. (2008). Event-related brain potential evidence for implicit change detection: a replication of Fernandez-Duque et al. (2003). *Neurosci. Lett.* 448, 236–239. doi: 10.1016/j.neulet.2008.10.064

Kinnunen, T., and Zamansky, H. S. (1996). Hypnotic amnesia and learning: a dissociation interpretation. *Am. J. Clin. Hypn.* 38, 247–253. doi: 10.1080/00029157.1996.10403348

Kirsch, I. (2011). The altered state issue: dead or alive? *Int. J. Clin. Exp. Hypn.* 59, 350–362. doi: 10.1080/00207144.2011.570681

Kirsch, I., Capafons, A., Cardeña-Buelna, E., and Amigó, S. (1999). *Clinical Hypnosis and Self-Regulation : Cognitive-behavioral Perspectives.* Washington, DC: American Psychological Association. doi: 10.1037/10282-000

Kirsch, I., and Lynn, S. J. (1995). The altered state of hypnosis – changes in the theoretical landscape. *Am. Psychol.* 50, 846–858. doi: 10.1037//0003-066x.50.10.846

Kirsch, I., and Lynn, S. J. (1998). Dissociation theories of hypnosis. *Psychol. Bull.* 123, 100–115. doi: 10.1037/0033-2909.123.1.100

Kiss, M., Van Velzen, J., and Eimer, M. (2008). The N2pc component and its links to attention shifts and spatially selective visual processing. *Psychophysiology* 45, 240–249. doi: 10.1111/j.1469-8986.2007.00611.x

Knapen, T., Brascamp, J., Pearson, J., van Ee, R., and Blake, R. (2011). The role of frontal and parietal brain areas in bistable perception. *J. Neurosci.* 31, 10293–10301. doi: 10.1523/JNEUROSCI.1727-11.2011

Koivisto, M., Hyönä, J., and Revonsuo, A. (2004). The effects of eye movements, spatial attention, and stimulus features on inattentional blindness. *Vision Res.* 44, 3211–3221. doi: 10.1016/j.visres.2004.07.026

Koivisto, M., Kirjanen, S., Revonsuo, A., and Kallio, S. (2013). A preconscious neural mechanism of hypnotically altered colors: a double case study. *PLoS ONE* 8:e70900. doi: 10.1371/journal.pone.0070900

Kornmeier, J., and Bach, M. (2006). Bistable perception – along the processing chain from ambiguous visual input to a stable percept. *Int. J. Psychophysiol.* 62, 345–349. doi: 10.1016/j.ijpsycho.2006.04.007

Kornmeier, J., and Bach, M. (2012). Ambiguous figures – what happens in the brain when perception changes but not the stimulus. *Front. Hum. Neurosci.* 6:51. doi: 10.3389/fnhum.2012.00051

Kosslyn, S. M., Thompson, W. L., Costantini-Ferrando, M. F., Alpert, N. M., and Spiegel, D. (2000). Hypnotic visual illusion alters color processing in the brain. *Am. J. Psychiatry* 157, 1279–1284. doi: 10.1176/appi.ajp.157.8.1279

Kouider, S., and Dehaene, S. (2007). Levels of processing during non-conscious perception: a critical review of visual masking. *Philos. Trans. R. Soc. B Biol. Sci.* 362, 857–875. doi: 10.1098/rstb.2007.2093

Kouider, S., Eger, E., Dolan, R., and Henson, R. N. (2009). Activity in face-responsive brain regions is modulated by invisible, attended faces: evidence from masked priming. *Cereb. Cortex* 19, 13–23. doi: 10.1093/cercor/bhn048

Koyama, T., McHaffie, J. G., Laurienti, P. J., and Coghill, R. C. (2005). The subjective experience of pain: where expectations become reality. *Proc. Natl. Acad. Sci. U.S.A.* 102, 12950–12955. doi: 10.1073/pnas.0408576102

Kramer, P., Massaccesi, S., Semenzato, L., Cecchetto, S., and Bressan, P. (2013). Motion-induced blindness measured objectively. *Behav. Res. Methods* 45, 267–271. doi: 10.3758/s13428-012-0246-5

Kranczioch, C., Debener, S., Schwarzbach, J., Goebel, R., and Engel, A. K. (2005). Neural correlates of conscious perception in the attentional blink. *Neuroimage* 24, 704–714. doi: 10.1016/j.neuroimage.2004.09.024

Laloyaux, C., Devue, C., Doyen, S., David, E., and Cleeremans, A. (2008). Undetected changes in visible stimuli influence subsequent decisions. *Conscious. Cogn.* 17, 646–656. doi: 10.1016/j.concog.2007.03.002

Lathrop, W. B., Bridgeman, B., and Tseng, P. (2011). Perception in the absence of attention: perceptual processing in the Roelofs effect during inattentional blindness. *Perception* 40, 1104–1119. doi: 10.1068/p6859

Lau, H. C., and Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 18763–18768. doi: 10.1073/pnas.0607716103

Leopold, D. A., and Logothetis, N. K. (1999). Multistable phenomena: changing views in perception. *Trends Cogn. Sci.* 3, 254–264. doi: 10.1016/S1364-6613(99)01332-7

Le Van Quyen, M., and Petitmengin, C. (2002). Neuronal dynamics and conscious experience: an example of reciprocal causation before epileptic seizures. *Phenomenol. Cogn. Sci.* 1, 169–180. doi: 10.1023/A:1020364003336

Levi, D. M. (2008). Crowding – an essential bottleneck for object recognition: a mini-review. *Vision Res.* 48, 635–654. doi: 10.1016/J.Visres.2007.12.009

Lifshitz, M., Aubert Bonn, N., Fischer, A., Kashem, I. F., and Raz, A. (2013). Using suggestion to modulate automatic processes: from Stroop to McGurk and beyond. *Cortex* 49, 463–473. doi: 10.1016/j.cortex.2012.08.007

Lifshitz, M., Campbell, N. K., and Raz, A. (2012). Varieties of attention in hypnosis and meditation. *Conscious. Cogn.* 21, 1582–1585. doi: 10.1016/j.concog.2012.05.008

Lin, Z., and He, S. (2009). Seeing the invisible: the scope and limits of unconscious processing in binocular rivalry. *Prog. Neurobiol.* 87, 195–211. doi: 10.1016/j.pneurobio.2008.09.002

Lipari, S., Baglio, F., Griffanti, L., Mendozzi, L., Garegnani, M., Motta, A., et al. (2012). Altered and asymmetric default mode network activity in a "hypnotic virtuoso": an fMRI and EEG study. *Conscious. Cogn.* 21, 393–400. doi: 10.1016/j.concog.2011.11.006

Long, G. M., and Toppino, T. C. (2004). Enduring interest in perceptual ambiguity: alternating views of reversible figures. *Psychol. Bull.* 130, 748–768. doi: 10.1037/0033-2909.130.5.748

Long, G. M., Toppino, T. C., and Mondin, G. W. (1992). Prime time: fatigue and set effects in the perception of reversible figures. *Percept. Psychophys.* 52, 609–616. doi: 10.3758/BF03211697

Luck, S. J., Vogel, E. K., and Shapiro, K. L. (1996). Word meanings can be accessed but not reported during the attentional blink. *Nature* 383, 616–618. doi: 10.1038/383616a0

Mack, A., and Rock, I. (1998). *Inattentional Blindness.* Cambridge, MA.: MIT Press.

MacLeod, C. M. (1991). Half a century of research on the Stroop effect: an integrative review. *Psychol. Bull.* 109, 163–203. doi: 10.1037/0033-2909.109.2.163

Mallard, D., and Bryant, R. A. (2001). Hypnotic color blindness and performance on the Stroop test. *Int. J. Clin. Exp. Hypn.* 49, 330–338. doi: 10.1080/00207140108410082

Marois, R., Yi, D.-J., and Chun, M. M. (2004). The neural fate of consciously perceived and missed events in the attentional blink. *Neuron* 41, 465–472. doi: 10.1016/S0896-6273(04)00012-1

Marshall, J. C., and Halligan, P. W. (1995). Seeing the forest but only half the trees? *Nature* 373, 521–523. doi: 10.1038/373521a0

Martens, S., Wolters, G., and van Raamsdonk, M. (2002). Blinks of the mind: memory effects of attentional processes. *J. Exp. Psychol. Hum. Percept. Perform.* 28, 1275–1287. doi: 10.1037/0096-1523.28.6.1275

Martens, S., and Wyble, B. (2010). The attentional blink: past, present, and future of a blind spot in perceptual awareness. *Neurosci. Biobehav. Rev.* 34, 947–957. doi: 10.1016/j.neubiorev.2009.12.005

Martens, U., Ansorge, U., and Kiefer, M. (2011). Controlling the unconscious attentional task sets modulate subliminal semantic and visuomotor processes differentially. *Psychol. Sci.* 22, 282–291. doi: 10.1177/0956797610397056

Marti, S., Sigman, M., and Dehaene, S. (2012). A shared cortical bottleneck underlying Attentional Blink and Psychological Refractory Period. *Neuroimage* 59, 2883–2898. doi: 10.1016/j.neuroimage.2011.09.063

Mazza, V., Turatto, M., and Caramazza, A. (2009). Attention selection, distractor suppression and N2pc. *Cortex* 45, 879–890. doi: 10.1016/j.cortex.2008.10.009

Mazzoni, G., Venneri, A., McGeown, W. J., and Kirsch, I. (2013). Neuroimaging resolution of the altered state hypothesis. *Cortex* 49, 400–410. doi: 10.1016/j.cortex.2012.08.005

McConkey, K. M., Glisky, M. L., and Kihlstrom, J. F. (1989). Individual differences among hypnotic virtuosos: a case comparison. *Aust. J. Clin. Exp. Hypn.* 17, 131–140.

McGeown, W. J., Mazzoni, G., Venneri, A., and Kirsch, I. (2009). Hypnotic induction decreases anterior default mode activity. *Conscious. Cogn.* 18, 848–855. doi: 10.1016/j.concog.2009.09.001

McGeown, W. J., Venneri, A., Kirsch, I., Nocetti, L., Roberts, K., Foan, L., et al. (2012). Suggested visual hallucination without hypnosis enhances activity in visual areas of the brain. *Conscious. Cogn.* 21, 100–116. doi: 10.1016/j.concog.2011.10.015

Memmert, D. (2006). The effects of eye movements, age, and expertise on inattentional blindness. *Conscious. Cogn.* 15, 620–627. doi: 10.1016/j.concog.2006.01.001

Mendelsohn, A., Chalamish, Y., Solomonovich, A., and Dudai, Y. (2008). Mesmerizing memories: brain substrates of episodic memory suppression in posthypnotic amnesia. *Neuron* 57, 159–170. doi: 10.1016/j.neuron.2007.11.022

Miller, M. F., Barabasz, A. F., and Barabasz, M. (1991). Effects of active alert and relaxation hypnotic inductions on cold pressor pain. *J. Abnorm. Psychol.* 100, 223–226. doi: 10.1037/0021-843X.100.2.223

Mlodinow, L. (2012). *Subliminal : How Your Unconscious Mind rules Your Behavior*, 1st Edn. New York: Pantheon Books.

Most, S. B. (2013). Setting sights higher: category-level attentional set modulates sustained inattentional blindness. *Psychol. Res.* 77, 139–146. doi: 10.1007/s00426-011-0379-7

Müller, K., Bacht, K., Prochnow, D., Schramm, S., and Seitz, R. J. (2013). Activation of thalamus in motor imagery results from gating by hypnosis. *Neuroimage* 66, 361–367. doi: 10.1016/j.neuroimage.2012.10.073

Müller, K., Bacht, K., Schramm, S., and Seitz, R. J. (2012). The facilitating effect of clinical hypnosis on motor imagery: An fMRI study. *Behav. Brain Res.* 231, 164–169. doi: 10.1016/j.bbr.2012.03.013

Naccache, L., Blandin, E., and Dehaene, S. (2002). Unconscious masked priming depends on temporal attention. *Psychol. Sci.* 13, 416–424. doi: 10.1111/1467-9280.00474

Naccache, L., Gaillard, R., Adam, C., Hasboun, D., Clemenceau, S., Baulac, M., et al. (2005). A direct intracranial record of emotions evoked by subliminal words. *Proc. Natl. Acad. Sci. U.S.A.* 102, 7713–7717. doi: 10.1073/Pnas.05005742102

Nandy, A. S., and Tjan, B. S. (2007). The nature of letter crowding as revealed by first-and second-order classification images. *J. Vis.* 7, 5.1–5.26. doi: 10.1167/7.2.5

Nash, M. R., and Barnier, A. J. (2008). *The Oxford Handbook of Hypnosis : Theory, Research and Practice.* Oxford: Oxford University Press.

Oakley, D. A. (2006). Hypnosis as a tool in research: experimental psychopathology. *Contemp. Hypn.* 23, 3–14. doi: 10.1002/ch.34

Oakley, D. A. (2008). "Hypnosis, trance and suggestion: Evidence from neuroimaging," in *Oxford Handbook of Hypnosis*, eds M. R. Nash and A. J. Barnier (Oxford: Oxford University Press), 365–392.

Oakley, D. A., and Halligan, P. W. (2009). Hypnotic suggestion and cognitive neuroscience. *Trends Cogn. Sci.* 13, 264–270. doi: 10.1016/j.tics.2009.03.004

Oakley, D. A., and Halligan, P. W. (2013). Hypnotic suggestion: opportunities for cognitive neuroscience. *Nat. Rev. Neurosci.* 14, 565–576. doi: 10.1038/nrn3538

Overgaard, M. (2011). Visual experience and blindsight: a methodological review. *Exp. Brain Res.* 209, 473–479. doi: 10.1007/s00221-011-2578-2

Overgaard, M., and Timmermans, B. (2010). "How unconscious is subliminal perception?," in *Handbook of Phenomenology and Cognitive Science*, 1st Edn, eds S. Gallagher and D. Schmicking (New York: Springer), 501–518.

Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., and Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nat. Neurosci.* 4, 739–744. doi: 10.1038/89532

Patterson, D. R., and Jensen, M. P. (2003). Hypnosis and clinical pain. *Psychol. Bull.* 129, 495–521. doi: 10.1037/0033-2909.129.4.495

Pelli, D. G., Palomares, M., and Majaj, N. J. (2004). Crowding is unlike ordinary masking: distinguishing feature integration from detection. *J. Vis.* 4, 1136–1169. doi: 10.1167/4.12.12

Pessoa, L., and Ungerleider, L. G. (2004). Neural correlates of change detection and change blindness in a working memory task. *Cereb. Cortex* 14, 511–520. doi: 10.1093/cercor/bhh013

Peter, B., Schiebler, P., Piesbergen, C., and Hagl, M. (2012). Electromyographic investigation of hypnotic arm levitation: differences between voluntary arm elevation and involuntary arm levitation. *Int. J. Clin. Exp. Hypn.* 60, 88–110. doi: 10.1080/00207144.2011.622213

Piccione, C., Hilgard, E. R., and Zimbardo, P. G. (1989). On the degree of stability of measured hypnotizability over a 25-year period. *J. Pers. Soc. Psychol.* 56, 289–295. doi: 10.1037/0022-3514.56.2.289

Ploghaus, A., Becerra, L., Borras, C., and Borsook, D. (2003). Neural circuitry underlying pain modulation: expectation, hypnosis, placebo. *Trends Cogn. Sci.* 7, 197–200. doi: 10.1016/S1364-6613(03)00061-5

Pourtois, G., De Pretto, M., Hauert, C.-A., and Vuilleumier, P. (2006). Time course of brain activity during change blindness and change awareness: performance is predicted by neural events before change onset. *J. Cogn. Neurosci.* 18, 2108–2129. doi: 10.1162/jocn.2006.18.12.2108

Price, D. D., and Rainville, P. (2013). "Hypnotic analgesia," in *Encyclopedia of Pain*, eds G. F. Genhart and R. F. Schmidt (New York: Springer-Verlag Berlin Heidelberg), 1537–1542.

Priftis, K., Schiff, S., Tikhonoff, V., Giordano, N., Amodio, P., Umilta, C., et al. (2011). Hypnosis meets neuropsychology: simulating visuospatial neglect in healthy participants. *Neuropsychologia* 49, 3346–3350. doi: 10.1016/j.neuropsychologia.2011.08.008

Rach, S., and Huster, R. J. (2014). In search of causal mechanisms underlying bistable perception. *J. Neurosci.* 34, 689–690. doi: 10.1523/JNEUROSCI.4811-13.2014

Rainville, P., Carrier, B., Hofbauer, R. K., Bushnell, M. C., and Duncan, G. H. (1999a). Dissociation of sensory and affective dimensions of pain using hypnotic modulation. *Pain* 82, 159–171. doi: 10.1016/S0304-3959(99)00048-2

Rainville, P., Hofbauer, R. K., Paus, T., Duncan, G. H., Bushnell, M. C., and Price, D. D. (1999b). Cerebral mechanisms of hypnotic induction and suggestion. *J. Cogn. Neurosci.* 11, 110–125. doi: 10.1162/089892999563175

Rainville, P., Duncan, G. H., Price, D. D., Carrier, B., and Bushnell, M. C. (1997). Pain affect encoded in human anterior cingulate but not somatosensory cortex. *Science* 277, 968–971. doi: 10.1126/science.277.5328.968

Rainville, P., Hofbauer, R. K., Bushnell, M. C., Duncan, G. H., and Price, D. D. (2002). Hypnosis modulates activity in brain structures involved in the regulation of consciousness. *J. Cogn. Neurosci.* 14, 887–901. doi: 10.1162/089892902760191117

Rainville, P., and Price, D. D. (2003). Hypnosis phenomenology and the neurobiology of consciousness. *Int. J. Clin. Exp. Hypn.* 51, 105–129. doi: 10.1076/iceh.51.2.105.14613

Raymond, J. E., Shapiro, K. L., and Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: an attentional blink? *J. Exp. Psychol. Hum. Percept. Perform.* 18, 849–860. doi: 10.1037/0096-1523.18.3.849

Raz, A. (2004). "Atypical attention: Hypnosis and conflict reduction," in *Cognitive Neuroscience of Attention*, ed. M. I. Posner (New York: Guilford Press).

Raz, A. (2011a). Does neuroimaging of suggestion elucidate hypnotic trance? *Int. J. Clin. Exp. Hypn.* 59, 363–377. doi: 10.1080/00207144.2011.570682

Raz, A. (2011b). Hypnosis: a twilight zone of the top-down variety Few have never heard of hypnosis but most know little about the potential of this mind-body regulation technique for advancing science. *Trends Cogn. Sci.* 15, 555–557. doi: 10.1016/j.tics.2011.10.002

Raz, A., Fan, J., and Posner, M. I. (2005). Hypnotic suggestion reduces conflict in the human brain. *Proc. Natl. Acad. Sci. U.S.A.* 102, 9978–9983. doi: 10.1073/pnas.0503064102

Raz, A., Lamar, M., Buhle, J. T., Kane, M. J., and Peterson, B. S. (2007). Selective biasing of a specific bistable-figure percept involves fMRI signal changes in frontostriatal circuits: a step toward unlocking the neural correlates of top-down control and self-regulation. *Am. J. Clin. Hypn.* 50, 137–156. doi: 10.1080/00029157.2007.10401611

Raz, A., and Michels, R. (2007). Contextualizing specificity: specific and non-specific effects of treatment. *Am. J. Clin. Hypn.* 50, 177–182. doi: 10.1080/00029157.2007.10401614

Raz, A., Shapiro, T., Fan, J., and Posner, M. I. (2002). Hypnotic suggestion and the modulation of Stroop interference. *Arch. Gen. Psychiatry* 59, 1155–1161. doi: 10.1001/archpsyc.59.12.1155

Raz, A., and Wolfson, J. B. (2010). From dynamic lesions to brain imaging of behavioral lesions: alloying the gold of psychoanalysis with the copper of suggestion. *Neuropsychoanalysis* 12, 5–18. doi: 10.1080/15294145.2010.10773621

Robitaille, N., and Jolicoeur, P. (2006). Fundamental properties of the N2pc as an index of spatial attention: effects of masking. *Can. J. Exp. Psychol.* 60, 101–111. doi: 10.1037/cjep2006011

Rolke, B., Heil, M., Streb, J., and Hennighausen, E. (2001). Missed prime words within the attentional blink evoke an N400 semantic priming effect. *Psychophysiology* 38, 165–174. doi: 10.1111/1469-8986.3820165

Sandberg, K., Timmermans, B., Overgaard, M., and Cleeremans, A. (2010). Measuring consciousness: is one measure better than the other? *Conscious. Cogn.* 19, 1069–1078. doi: 10.1016/j.concog.2009.12.013

Sanguinetti, J. L., Allen, J. J., and Peterson, M. A. (2013). The ground side of an object: perceived as shapeless yet processed for semantics. *Psychol. Sci.* doi: 10.1177/0956797613502814 [Epub ahead of print].

Schankin, A., and Wascher, E. (2007). Electrophysiological correlates of stimulus processing in change blindness. *Exp. Brain Res.* 183, 95–105. doi: 10.1007/s00221-007-1023-z

Schnyer, D. M., and Allen, J. J. (1995). Attention-related electroencephalographic and event-related potential predictors of responsiveness to suggested posthypnotic amnesia. *Int. J. Clin. Exp. Hypn.* 43, 295–315. doi: 10.1080/00207149508409972

Scholvinck, M. L., and Rees, G. (2009). Attentional influences on the dynamics of motion-induced blindness. *J. Vis.* 9, 38.31–38.39. doi: 10.1167/9.1.38

Sebastiani, L., D'Alessandro, L., Menicucci, D., Ghelarducci, B., and Santarcangelo, E. L. (2007). Role of relaxation and specific suggestions in hypnotic emotional numbing. *Int. J. Psychophysiol.* 63, 125–132. doi: 10.1016/j.ijpsycho.2006.10.001

Sergent, C., Baillet, S., and Dehaene, S. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nat. Neurosci.* 8, 1391–1400. doi: 10.1038/nn1549

Seth, A. K., Dienes, Z., Cleeremans, A., Overgaard, M., and Pessoa, L. (2008). Measuring consciousness: relating behavioural and neurophysiological approaches. *Trends Cogn. Sci.* 12, 314–321. doi: 10.1016/j.tics.2008.04.008

Shapiro, K. L., Driver, J., Ward, R., and Sorensen, R. E. (1997a). Priming from the attentional blink: a failure to extract visual tokens but not visual types. *Psychol. Sci.* 8, 95–100. doi: 10.1111/j.1467-9280.1997.tb00689.x

Shapiro, K. L., Raymond, J. E., and Arnell, K. M. (1997b). The attentional blink. *Trends Cogn. Sci.* 1, 291–296. doi: 10.1016/S1364-6613(97)01094-2

Shapiro, K. L., Hillstrom, A. P., and Husain, M. (2002). Control of visuotemporal attention by inferior parietal and superior temporal cortex. *Curr. Biol.* 12, 1320–1325. doi: 10.1016/S0960-9822(02)01040-0

Shimaoka, D., and Kaneko, K. (2011). Dynamical systems modeling of continuous flash suppression. *Vision Res.* 51, 521–528. doi: 10.1016/j.visres.2011.01.009

Silverman, M. E., and Mack, A. (2006). Change blindness and priming: when it does and does not occur. *Conscious. Cogn.* 15, 409–422. doi: 10.1016/j.concog.2005.08.003

Simons, D. J. (2000). Attentional capture and inattentional blindness. *Trends Cogn. Sci.* 4, 147–55. doi: 10.1016/S1364-6613(00)01455-8

Simons, D. J., and Chabris, C. F. (1999). Gorillas in our midst: sustained inattentional blindness for dynamic events. *Perception* 28, 1059–1074. doi: 10.1068/p2952

Simons, D. J., and Levin, D. T. (1997). Change blindness. *Trends Cogn. Sci.* 1, 261–267. doi: 10.1016/S1364-6613(97)01080-2

Simons, D. J., and Levin, D. T. (1998). Failure to detect changes to people during a real-world interaction. *Psychon. Bull. Rev.* 5, 644–649. doi: 10.3758/BF03208840

Simons, D. J., and Rensink, R. A. (2005). Change blindness: past, present, and future. *Trends Cogn. Sci.* 9, 16–20. doi: 10.1016/j.tics.2004.11.006

Spanos, N. P., Radtke, H. L., and Dubreuil, D. L. (1982). Episodic and semantic memory in posthypnotic amnesia: a reevaluation. *J. Pers. Soc. Psychol.* 43, 565–573. doi: 10.1037/0022-3514.43.3.565

Spanos, N. P., Rivers, S. M., and Ross, S. (1977). Experienced involuntariness and response to hypnotic suggestions. *Ann. N. Y. Acad. Sci.* 296, 208–221. doi: 10.1111/j.1749-6632.1977.tb38173.x

Spiegel, D. (2003). Negative and positive visual hypnotic hallucinations: attending inside and out. *Int. J. Clin. Exp. Hypn.* 51, 130–146. doi: 10.1076/iceh.51.2.130.14612

Sterzer, P., Jalkanen, L., and Rees, G. (2009a). Electromagnetic responses to invisible face stimuli during binocular suppression. *Neuroimage* 46, 803–808. doi: 10.1016/j.neuroimage.2009.02.046

Sterzer, P., Kleinschmidt, A., and Rees, G. (2009b). The neural bases of multistable perception. *Trends Cogn. Sci.* 13, 310–318. doi: 10.1016/j.tics.2009.04.006

Sterzer, P., Stein, T., Ludwig, K., Rothkirch, M., and Hesselmann, G. (2014). Neural processing of visual information under interocular suppression: a critical review. *Front. Psychol.* 5:453. doi: 10.3389/fpsyg.2014.00453

Tallis, F. (2002). Hidden Minds : *A History of the Unconscious*, 1st North American Edn. New York: Arcade Pub.

Tallon-Baudry, C. (2011). On the neural mechanisms subserving consciousness and attention. *Front. Psychol.* 2:397. doi: 10.3389/fpsyg.2011.00397

Terhune, D. B., Cardeña, E., and Lindgren, M. (2010). Disruption of synaesthesia by posthypnotic suggestion: an ERP study. *Neuropsychologia* 48, 3360–3364. doi: 10.1016/j.neuropsychologia.2010.07.004

Terhune, D. B., Cardeña, E., and Lindgren, M. (2011). Dissociated control as a signature of typological variability in high hypnotic suggestibility. *Conscious. Cogn.* 20, 727–736. doi: 10.1016/j.concog.2010.11.005

Thakral, P. P. (2011). The neural substrates associated with inattentional blindness. *Conscious. Cogn.* 20, 1768–1775. doi: 10.1016/j.concog.2011.03.013

Thakral, P. P., and Slotnick, S. D. (2010). Attentional inhibition mediates inattentional blindness. *Conscious. Cogn.* 19, 636–643. doi: 10.1016/j.concog.2010.02.002

Tong, F., Meng, M., and Blake, R. (2006). Neural bases of binocular rivalry. *Trends Cogn. Sci.* 10, 502–511. doi: 10.1016/j.tics.2006.09.003

Toppino, T. C., and Long, G. M. (2005). "Top-down and bottom-up processes in the perception of reversible figures: toward a hybrid model," in *Dynamic Cognitive Processes,* eds N. Ohta, C. M. MacLeod and B. Uttl (Tokyo: Springer), 37–58.

Tseng, P., Hsu, T.-Y., Muggleton, N. G., Tzeng, O. J. L., Hung, D. L., and Juan, C.-H. (2010). Posterior parietal cortex mediates encoding and maintenance processes in change blindness. *Neuropsychologia* 48, 1063–1070. doi: 10.1016/j.neuropsychologia.2009.12.005

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Tsuchiya, N., Koch, C., Gilroy, L. A., and Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *J. Vis.* 6, 1068–1078. doi: 10.1167/6.10.6

van Boxtel, J. J. A., Tsuchiya, N., and Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. *Proc. Natl. Acad. Sci. U.S.A.* 107, 8883–8888. doi: 10.1073/pnas.0913292107

Van den Bussche, E., Notebaert, K., and Reynvoet, B. (2009a). Masked primes can be genuinely semantically processed: a picture prime study. *Exp. Psychol.* 56, 295–300. doi: 10.1027/1618-3169.56.5.295

Van den Bussche, E., Van den Noortgate, W., and Reynvoet, B. (2009b). Mechanisms of masked priming: a meta-analysis. *Psychol. Bull.* 135, 452–477. doi: 10.1037/a0015329

van Gaal, S., and Lamme, V. A. F. (2012). Unconscious high-level information processing implication for neurobiological theories of consciousness. *Neuroscientist* 18, 287–301. doi: 10.1177/1073858411404079

Vanhaudenhuyse, A., Boly, M., Balteau, E., Schnakers, C., Moonen, G., Luxen, A., et al. (2009). Pain and non-pain processing during hypnosis: a thulium-YAG event-related fMRI study. *Neuroimage* 47, 1047–1054. doi: 10.1016/j.neuroimage.2009.05.031

Varga, K., Nemeth, Z., and Szekely, A. (2011). Lack of correlation between hypnotic susceptibility and various components of attention. *Conscious. Cogn.* 20, 1872–1881. doi: 10.1016/J.Concog.2011.09.008

Vermersch, P. (1994). *L'entretien d'explicitation.* Paris: ESF éditeur.

Wallis, T. S., and Arnold, D. H. (2009). Motion-induced blindness and motion streak suppression. *Curr. Biol.* 19, 325–329. doi: 10.1016/j.cub.2008.12.053

Ward, N. S., Oakley, D. A., Frackowiak, R. S. J., and Halligan, P. W. (2003). Differential brain activations during intentionally simulated and subjectively experienced paralysis. *Cogn. Neuropsychiatry* 8, 295–312. doi: 10.1080/13546800344000200

Weilnhammer, V. A., Ludwig, K., Hesselmann, G., and Sterzer, P. (2013). Frontoparietal cortex mediates perceptual transitions in bistable perception. *J. Neurosci.* 33, 16009–16015. doi: 10.1523/JNEUROSCI.1418-13.2013

Weiskrantz, L. (1986). *Blindsight: A Case Study and Implications.* Oxford: Clarendon Press.

Wenzlaff, R. M., and Wegner, D. M. (2000). Thought suppression. *Annu. Rev. Psychol.* 51, 59–91. doi: 10.1146/annurev.psych.51.1.59

Whitney, D., and Levi, D. M. (2011). Visual crowding: a fundamental limit on conscious perception and object recognition. *Trends Cogn. Sci.* 15, 160–168. doi: 10.1016/j.tics.2011.02.005

Wiemer, J., Gerdes, A. B. M., and Pauli, P. (2013). The effects of an unexpected spider stimulus on skin conductance responses and eye movements: an inattentional blindness study. *Psychol. Res.* 77, 155–166. doi: 10.1007/s00426-011-0407-7

Wixted, J. T., and Squire, L. R. (2011). The medial temporal lobe and the attributes of memory. *Trends Cogn. Sci.* 15, 210–217. doi: 10.1016/j.tics.2011.03.005

Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Res.* 24, 471–478. doi: 10.1016/0042-6989(84)90044-0

Woodman, G. F., Arita, J. T., and Luck, S. J. (2009). A cuing study of the N2pc component: an index of attentional deployment to objects rather than spatial locations. *Brain Res.* 1297, 101–111. doi: 10.1016/j.brainres.2009.08.011

Woody, E., Lewis, V., Snider, L., Grant, H., Kamath, M., and Szechtman, H. (2005). Induction of compulsive-like washing by blocking the feeling of knowing: an experimental test of the security-motivation hypothesis of obsessive-compulsive disorder. *Behav. Brain Funct.* 1, 11. doi: 10.1186/1744-9081-1-11

Woody, E., and Sadler, P. (2008). "Dissociation theories of hypnosis," in *The Oxford Handbook of Hypnosis*, eds M. R. Nash and A. J. Barnier (Oxford: Oxford University Press), 81–110.

Woody, E., and Szechtman, H. (2011). Using hypnosis to develop and test models of psychopathology. *J. Mind Body Regul.* 1, 4–16.

Yang, E., and Blake, R. (2012). Deconstructing continuous flash suppression. *J. Vis.* 12, 8. doi: 10.1167/12.3.8

Yeh, S.-L., He, S., and Cavanagh, P. (2012). Semantic priming from crowded words. *Psychol. Sci.* 23, 608–616. doi: 10.1177/0956797611434746

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 08 April 2014; accepted: 03 July 2014; published online: 28 July 2014.
Citation: Landry M, Appourchaux K and Raz A (2014) Elucidating unconscious processing with instrumental hypnosis. Front. Psychol. ***5****:785. doi: 10.3389/fpsyg.2014.00785*
This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

REVIEW ARTICLE
published: 11 July 2014
doi: 10.3389/fpsyg.2014.00724

On the use of continuous flash suppression for the study of visual processing outside of awareness

Eunice Yang*[1] *, *Jan Brascamp*[2], *Min-Suk Kang*[3,4] and *Randolph Blake*[5,6]

[1] School of Optometry, University of California at Berkeley, Berkeley, CA, USA
[2] Helmholtz Institute and Division of Experimental Psychology, Department of Psychology, Utrecht University, Utrecht, Netherlands
[3] Department of Psychology, Sungkyunkwan University, Seoul, Republic of Korea
[4] Center for Neuroscience Imaging Research, Institute for Basic Science, Daejeon, Republic of Korea
[5] Department of Psychology, Vanderbilt University, Nashville, TN, USA
[6] Department of Brain and Cognitive Sciences, Seoul National University, Seoul, Republic of Korea

Edited by:
Julien Dubois, California Institute of Technology, USA

Reviewed by:
Naotsugu Tsuchiya, Monash University, Australia
Timo Stein, University of Trento, Italy

****Correspondence:***
Eunice Yang, School of Optometry, University of California at Berkeley, 487 Minor Hall, Berkeley, CA 94720, USA
e-mail: eunice.yang21@gmail.com

The interocular suppression technique termed continuous flash suppression (CFS) has become an immensely popular tool for investigating visual processing outside of awareness. The emerging picture from studies using CFS is that extensive processing of a visual stimulus, including its semantic and affective content, occurs despite suppression from awareness of that stimulus by CFS. However, the current implementation of CFS in many studies examining processing outside of awareness has several drawbacks that may be improved upon for future studies using CFS. In this paper, we address some of those shortcomings, particularly ones that affect the assessment of unawareness during CFS, and ones to do with the use of "visible" conditions that are often included as a comparison to a CFS condition. We also discuss potential biases in stimulus processing as a result of spatial attention and feature-selective suppression. We suggest practical guidelines that minimize the effects of those limitations in using CFS to study visual processing outside of awareness.

Keywords: continuous flash suppression, binocular rivalry, interocular suppression, unconscious processing, visual processing

INTRODUCTION

During our waking hours our eyes provide us with more sensory information than we can possibly process in detail, and only a small proportion of this information reaches awareness. At the same time, it would be adaptive for our brains to continue monitoring potentially relevant sensory signals, even those that do not culminate in a conscious experience. Indeed, several lines of research suggest that unperceived visual information can influence perceptual and cognitive operations, without our awareness (reviews by Bridgeman, 1992; Merikle and Daneman, 1998; Goodale and Milner, 2004).

While the notion of processing outside of awareness[1] is intriguing, it remains one of the most controversial issues in psychology, and for decades the research area has been fraught with methodological and theoretical challenges (e.g., Eriksen, 1960; Marcel, 1983; Holender, 1986; Merikle and Daneman, 1998). Yet at the same time, psychophysical techniques for rendering stimuli perceptually invisible continue to be developed, providing researchers with an ever more varied array of experimental tools for investigating processing outside of awareness (review by Kim and Blake, 2005). Some of these tools exploit the reflexive suppression that occurs when different images are simultaneously presented to the two eyes, i.e., dichoptic stimulation. An advantage of dichoptic stimulation techniques over other approaches is that an observer can monocularly view one of any variety of salient stimuli, yet remain unaware of its presence for seconds at a time. Variants of this dichoptic stimulation technique include binocular rivalry (Wheatstone, 1838; Breese, 1909), flash suppression (Wolfe, 1984), generalized flash suppression (Wilke et al., 2003), flicker-swap rivalry (Logothetis et al., 1996), and binocular switch suppression (Arnold et al., 2008). One version that has recently become popular as a means for erasing visual stimuli from awareness is called continuous flash suppression (CFS; Tsuchiya and Koch, 2005), and it is the focus of our paper.

While traditional binocular rivalry typically involves two displays of roughly similar "potency" (e.g., comparable motion content and luminance contrast) being presented to the two eyes, CFS critically involves a much less balanced design. During CFS one eye views rapidly flashing contour-rich patterns of high contrast (sometimes referred to as dynamic Mondrians), while the other views a stimulus that is typically stationary and of moderate contrast. The ever-changing patterns viewed by one eye cause periods of invisibility of the unchanging stimulus viewed by the other eye, and these periods can last for dozens of seconds, about 10 times longer than suppression produced with traditional binocular rivalry (Tsuchiya and Koch, 2005). CFS has several attractive features. For instance, anecdotal observations by several laboratories indicate that the suppressive effect of CFS can engulf even

---

[1] We prefer the phrase "processing outside of awareness" to "unconscious processing" because the latter could be confused to imply that we are focusing on neural correlates of consciousness. Our focus is exclusively on the extent to which a visual stimulus remains effective when it is erased temporarily from visual awareness.

relatively large stimuli presented to the other eye, stimuli that yield pronounced piecemeal suppression when viewed during binocular rivalry (e.g., Meenes, 1930; Blake et al., 1992). In addition, with CFS complete invisibility can reliably be induced from the very onset of stimulus presentation, in contrast to the situation during traditional binocular rivalry where the initially suppressed stimulus can be unpredictable (e.g., Carter and Cavanagh, 2007; Song and Yao, 2009) and subsequent fluctuations in suppression transpire unpredictably between the two rival stimuli (e.g., Fox and Herrmann, 1967). While masking and attentional blink paradigms, like CFS, allow control over the onset timing of invisibility, those two techniques are constrained by allowing only very brief stimulus durations (Kim and Blake, 2005). Furthermore, in comparison to paradigms like crowding and motion induced blindness, perceptual suppression with CFS is less susceptible to the effects of unstable fixation and eye movements (Kim and Blake, 2005). Given these properties of the perceptual suppression induced by CFS, it is not surprising that CFS has been quickly and widely adopted as a tool for investigating visual processing outside of awareness.

When looking at findings from studies using CFS, the evidence for stimulus processing outside of awareness seems compelling. As reviewed below, CFS suppression does not appear to preclude neural processing, either of low-level stimulus features, or of abstract stimulus properties with dedicated representations at more advanced stages of the visual system. In the case of low-level features, the notion that these are registered outside of awareness has also been confirmed using a number of other perceptual suppression techniques, including traditional binocular rivalry. With regard to more advanced stages of analysis, however, the picture from the literature as a whole is worth revisiting, given that there is little evidence for high-level processing during suppression phases of traditional binocular rivalry which, ironically, is reputed to create weaker interocular suppression than does CFS (Tsuchiya and Koch, 2005; Tsuchiya et al., 2006).

In addition to this apparent discrepancy between CFS and traditional binocular rivalry, another motivation behind this review is our conviction that CFS experiments into processing outside of awareness, although often straightforward in their basic idea, are surprisingly complicated, and their design and interpretation are fraught with subtleties. Careful consideration of these subtleties is particularly important because work that uses CFS for this purpose may have a significant impact on current theories of neural information processing, emotional processing, and psychopathology. Indeed, the utilization of CFS has already found its way into clinical research (Sterzer et al., 2011; Sylvers et al., 2011; Yang et al., 2011), and so it is imperative that CFS be used wisely to study processing outside of awareness.

The objective of our paper is to recommend practical guidelines for researchers interested in exploring this technique as a means of investigating stimulus processing outside of awareness. Our recommendations are centered on answering four primary questions:

(1) What are suitable paradigms to use with CFS to study processing outside of awareness?
(2) What are the optimal ways to determine whether a stimulus is genuinely invisible?
(3) What are effective methods for gaging the specificity and strength of stimulus processing outside of awareness?
(4) What are factors that influence the robustness of stimulus-driven effects under CFS?

We draw attention to several considerations that should be made when answering each of these questions. For the first question, we review the common approaches used to study processing outside of awareness with CFS. For the second question, we reexamine the methods used to assess observers' perception during CFS suppression, since evidence for processing outside of awareness rests critically on demonstrating absence of awareness. This is particularly pertinent to behavioral priming and adaptation paradigms as well as neurophysiological studies that use CFS to examine stimulus processing outside of awareness. For the third question, we discuss the application of "visible" conditions used to provide a comparison for CFS conditions in order to determine the specificity and strength of stimulus-driven effects during CFS. For the fourth question, we discuss mechanisms that can potentially modulate stimulus processing under CFS such as those engaged in attention and feature-selective suppression. Following the discussion of each issue, we propose strategies for effectively resolving these questions and for minimizing methodological confounds in using CFS to study processing outside of awareness.

From the outset we acknowledge that the matter of "processing outside of awareness" is fraught with controversy, with sharp points of disagreement within the field. Our views are unlikely to be received without question by all who are interested in this issue. We do hope that our views can advance the conversation in a constructive way.

WHAT ARE SUITABLE PARADIGMS TO USE WITH CFS TO STUDY PROCESSING OUTSIDE OF AWARENESS?

In this section, we review research that has used CFS to ask whether visual processing can transpire outside of awareness (**Figure 1**). We focus on three types of behavioral effects that have been investigated to tackle this question: (1) adaptation aftereffects of suppressed stimuli, (2) priming effects evoked by suppressed stimuli, and (3) dependence of suppression duration on the nature of the suppressed stimulus. In each case we will also briefly address how recent CFS findings compare to previous findings obtained using traditional binocular rivalry.

Adaptation aftereffects with CFS

Several CFS studies have utilized the well-established adaptation paradigm in which exposure to a stimulus gives rise to visual aftereffects (**Figure 1A**). A variety of different aftereffects exist, each specifically affecting detection or appearance of particular stimulus attributes, ranging from low-level properties such as orientation (e.g., the tilt aftereffect) to high-level features such as face identity and facial expression. Aftereffects have been widely used psychophysically to isolate and probe neural mechanisms involved in processing particular stimulus attributes (Mollon, 1974; Thompson and Burr, 2009). One way to investigate the extent of stimulus encoding outside of

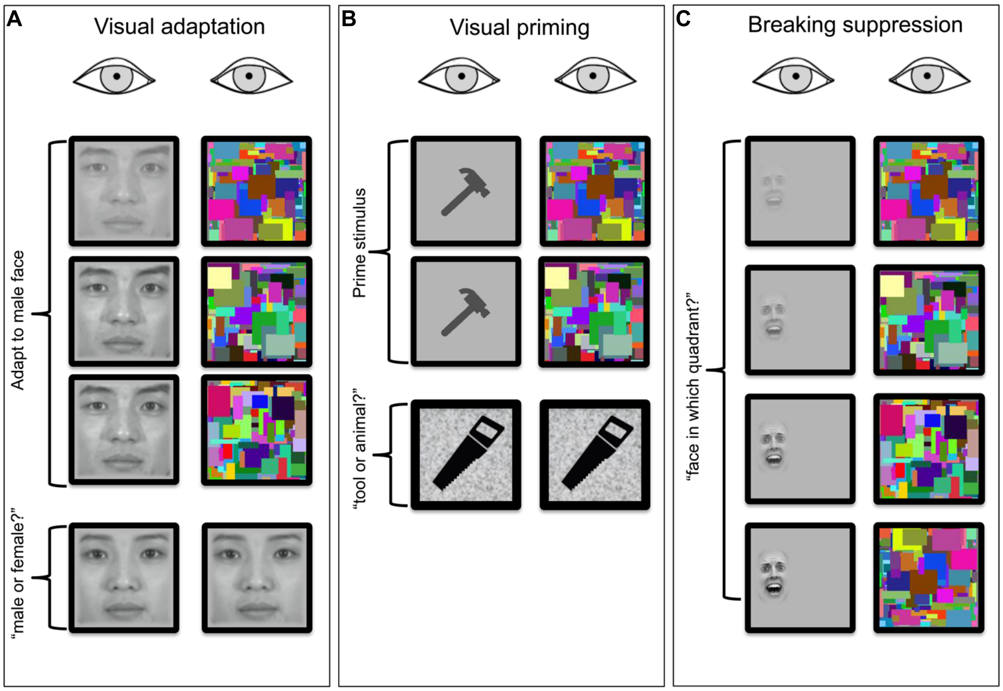


FIGURE 1 | Schematics of three frequently employed test procedures for assessing the effect of interocular suppression induced by CFS on visual processing. In all three panels, time runs from the top to the bottom. **(A)** Visual adaptation stimulus (a male face in this example) is presented to one eye for a duration ordinarily sufficient to generate a visual aftereffect (shift in perceived gender of neutral test face viewed following adaptation). Is the aftereffect attenuated or abolished consequent to suppression of awareness of the male face by the CFS array viewed by the other eye? The adapting face is turned on gradually over several hundred milliseconds to avoid abrupt transients that can briefly perturb suppression (Photographs courtesy of Sang Chul Chong, Yonsei University). **(B)** Visual priming stimulus is briefly presented to one eye while the other eye views a CFS array. Does this prime stimulus influence accuracy and/or speed of performance on a subsequent object categorization task? **(C)** bCSF trial where a stimulus presented to one eye remains present until the observer has sufficient information to specify the location of the target (in this example a 2AFC detection task). In one variant of this b-CFS task, the observer is simply asked to indicate when the monocular stimulus achieves dominance. With b-CFS the experimenter is usually interested in learning whether provocative (e.g., fearful face) or atypical (e.g., inverted face) stimuli yield significantly different times-to-dominance compared to putatively neutral versions of the same class of stimuli (Face © Bantosh/ CC-BY-SA-3.0).

awareness is to determine whether aftereffects can be induced and, by inference, whether neural adaptation occurs, when the inducing stimulus is suppressed from awareness during the adaptation period. If full-strength adaptation aftereffects can be induced despite perceptual suppression, it stands to reason that the neural events responsible for adaptation transpire regardless of observers' awareness of the inducing stimulus. On the other hand, these neural events may be affected by suppression, resulting in aftereffects that are weakened or even abolished (Blake et al., 2006). Considering that induction of strong aftereffects typically requires longer periods of visual adaptation, CFS – because of the enduring suppression it produces – is particularly suitable for testing adaptation aftereffects of invisible stimuli.

In some cases when this strategy was applied with CFS to suppress an adapting stimulus, CFS effectively weakened, but not necessarily abolished, the resulting adaptation aftereffect. This is true for aftereffects specific to stimulus properties often ascribed to early visual processing, including spatial phase (van Boxtel et al., 2010b), orientation (Kanai et al., 2006; Bahrami et al., 2008), motion (Maruya et al., 2008; Kaunitz et al., 2011a), and contrast (Shin et al., 2009; Yang et al., 2010b). At the same time, aftereffects thought to result from adaptation within "high-level" stages of visual processing are typically abolished entirely by suppression – examples in this category include aftereffects induced by adaptation to complex motion (Maruya et al., 2008; Kaunitz et al., 2011a), to curvature (Sweeny et al., 2011) and to faces specific for race (Amihai et al., 2011), for gender (Shin et al., 2009; Amihai et al., 2011), for gaze (Stein et al., 2012a), for face shape (Stein and Sterzer, 2011), and for emotional expression (Yang et al., 2010b; but see Adams et al., 2010). The attenuation of early visual adaptation and the complete disruption of high-level visual adaptation during CFS are fairly consistent with results obtained using the adaptation aftereffect paradigm in conjunction with traditional binocular rivalry (see Blake and He, 2005 for review).

Studies of adaptation aftereffects clearly demonstrate that CFS interferes with the neural analysis of diverse stimulus attributes. Moreover, if suppression greatly influences encoding of fundamental visual properties such as orientation and contrast, one could reasonably assume that it would similarly affect encoding of more complex image properties that are defined by combinations of these features. However, other lines of research suggest that certain classes of complex properties continue to be processed despite being blocked from visual awareness by CFS. One source of support is evidence of priming effects from stimuli suppressed with CFS, the topic we turn to next.

Priming effects with CFS

Subliminal priming procedures are among the most established and most popular techniques used to investigate visual processing outside of awareness (**Figure 1B**). These procedures build on traditional priming paradigms that demonstrate improved performance on tasks that involve a target stimulus, when presentation of that stimulus is preceded by presentation of a (prime) stimulus that shares physical or conceptual (semantic) characteristics of the target stimulus (Marcel, 1983; reviews by Snodgrass et al., 2004; Kouider and Dehaene, 2007). When the prime stimulus is suppressed from awareness but nonetheless engenders a priming effect on the subsequently viewed target, the presumption is that the stimulus feature or characteristic responsible for priming has been neurally registered despite the phenomenological suppression of the prime.

In various studies using CFS as the agent of suppression, invisible primes remained effective on tasks where the target was identical to the prime (Faivre et al., 2012), on tasks where the targets were semantically or categorically related to the prime (Almeida et al., 2008, 2010; Zabelina et al., 2013; but see Kang et al., 2011; Sakuraba et al., 2012), and on tasks where the targets were similar in their numerosity (Bahrami et al., 2010). To give one specific example, Almeida et al. (2008) presented images of objects drawn from different categories (i.e., animals, tools, vehicles) as prime and target stimuli, and prime stimuli were rendered invisible owing to CFS. Observers' reaction times (RTs) in categorizing targets were reduced when these were objects in the tool category that were preceded by an invisible prime that was also a tool, but this priming effect was not found for the other object categories. This category-specific priming effect suggests that objects in the tool category may be preferentially processed without awareness. Another set of findings demonstrated that emotional expressions presented under CFS biased observers' preference toward subsequently presented neutral stimuli (Anderson et al., 2012; Almeida et al., 2013; but see Faivre et al., 2012; de Zilva et al., 2013). These results indicate that stimuli presented outside of awareness can undergo analysis specific to relatively abstract properties like numerosity, object category and emotional content, thus leading to observable perceptual or decisional biases.

Unlike the situation for the literature on aftereffects and CFS, results on priming and CFS seem at odds with the pattern of findings reported when traditional binocular rivalry is used to manipulate awareness. In contrast to the CFS findings described above, both semantic priming effects with words and repetition priming effects with pictorial images were found to be completely abolished when prime stimuli were suppressed under binocular rivalry (Zimba and Blake, 1983; Cave et al., 1998). Considering that CFS is a stronger form of interocular suppression than binocular rivalry (Tsuchiya et al., 2006) one would, if anything, expect the effectiveness of a suppressed prime stimulus to be even weaker in the case of CFS. The source of this discrepancy between CFS and binocular rivalry priming studies has yet to be elucidated, but one factor to keep in mind pertains to the temporal buildup of suppression produced by CFS. Tsuchiya et al. (2006) found that the potency of suppression is initially relatively weak and builds up with successive mask presentations, plateauing after about 500 ms (i.e., the appearance of five successive masks). Therefore suppression may be shallow at shorter presentation durations of the CFS display, which happen to be adopted by some priming studies (Almeida et al., 2008, 2010, 2013; Sakuraba et al., 2012).

Emergence from suppression with CFS

The third and final line of research discussed here that utilizes CFS in investigating processing outside of awareness entails measuring the amount of time that a stimulus remains suppressed under CFS (**Figure 1C**). The assumption in these studies is that particular stimuli or categories of stimuli that emerge more quickly from suppression, relative to other stimuli, are being registered despite being suppressed owing to CFS. Unlike adaptation and priming paradigms in which stimulus awareness and behavioral effects driven by processes outside of awareness are measured independently, the "breaking continuous flash suppression" (b-CFS) technique provides a measure of stimulus awareness with which one may be able to infer processing outside of awareness. As a result of this property of b-CFS, there exists disagreement in the literature regarding the extent to which b-CFS actually provides a valid measure of unconscious processing (Stein et al., 2011b).

Breaking continuous flash suppression is based on a hallmark characteristic of binocular rivalry: stronger stimuli (e.g., high contrast stimulus) remain suppressed for shorter periods of time (Levelt, 1965). Using this technique, Jiang et al. (2007) presented either upright or inverted face stimuli to an observer's suppressed eye while a CFS mask was presented to the other eye, and they measured the time it took for the observer to report the location of the face as it emerged from suppression. Upright faces were detected faster than inverted faces (also see Yang et al., 2007; Stein et al., 2011b), implying that upright faces were effectively stronger stimuli than inverted faces. Jiang et al. (2007) interpreted this result to mean that invisible upright faces were processed at the level of object category, given that basic stimulus features do not vary importantly with variations in face orientation whereas face recognition is highly susceptible to face orientation. This finding has inspired others to investigate processing outside of awareness of social and emotional cues of faces using the same CFS technique. These studies have found that faces with fearful expressions tend to break suppression more quickly than other facial expressions (Yang et al., 2007; Tsuchiya et al., 2009; Sterzer et al., 2011; Gray et al., 2013; Stein et al., 2014), as do faces with eyes that gaze directly at the observer (Stein et al., 2011a) and faces judged as trustworthy or as non-domineering (Stewart et al., 2012).

Breaking continuous flash suppression has also been used to examine whether other high-level properties, including lexical and semantic information, are processed outside of awareness. For instance, images of morphemes that are part of one's native language tend to emerge from suppression faster than images of unfamiliar, foreign words (Jiang et al., 2007). Similarly, an initially suppressed word breaks suppression more quickly if that word is preceded by a semantically related visible word (Costello et al., 2009). The affective connotation of a word or phrase may also modulate the duration of suppression under CFS (Yang and Yeh, 2010; Sklar et al., 2012). Finally, the time to break from suppression is also reduced for stimuli that are semantically congruent with concurrently presented stimuli delivered through another sensory modality – this bisensory facilitation is found with hearing (Alsius and Munhall, 2013; Lupyan and Ward, 2013) and with olfaction (Zhou et al., 2010). Overall, the existing evidence implies that with b-CFS, semantic information of an invisible stimulus may be encoded and, consequently, strengthen the neural signals associated with that stimulus, empowering it to emerge more quickly from suppression.

Again we can compare these results obtained using b-CFS with those found using traditional binocular rivalry. Binocular rivalry findings are similar in showing that cognitively salient (i.e., meaningful) stimuli exhibit predominance over less meaningful stimuli (Walker, 1978; review by Blake and Logothetis, 2002). For example, recognizable figures (Yu and Blake, 1992), familiar images (Engel, 1956; Losciuto and Hartley, 1963), and emotional faces (e.g., Alpers and Gerdes, 2007; Bannerman et al., 2008) enjoy prolonged perceptual dominance. Note, however, an important difference between the measures of "time to break from suppression" during b-CFS and predominance during binocular rivalry. Because binocular rivalry involves alternating perception of both eyes' images, changes in predominance can often be explained by altered processing of the perceptually dominant stimulus rather than any processing occurring in the suppression phase of rivalry. Indeed it is well-established that, for instance, attention to the perceptually dominant stimulus increases its dominance durations (Lack, 1978; Ooi and He, 1999; Meng and Tong, 2004; Chong et al., 2005; Hugrass and Crewther, 2012). In this sense, the time a stimulus takes to break initial suppression during b-CFS can provide a more unequivocal answer than can binocular rivalry, depending on the question being asked. It is also worth noting that binocular rivalry studies using test probe techniques often rely on stimulus discrimination (e.g., Ling and Blake, 2009) or recognition (e.g., Alais and Melcher, 2007) to gage the depth of suppression whereas b-CFS studies tend to use detection or stimulus localization. Different tasks could contribute to apparent differences in interpretation of results from rivalry and b-CFS.

Recommendations

Adaptation, priming, and b-CFS are all adapted from well-established techniques in studying stimulus processing. Priming and b-CFS techniques may be suitable for investigating both perceptual and higher-level cognitive processes outside of awareness, whereas visual adaptation may be optimal for examining predominantly low-level visual processes and some complex ones as well (i.e., face processing). Before deciding which technique to use, experimenters should also consider the shortcomings of the current implementation of each technique, which are discussed throughout the remaining parts of this paper.

WHAT ARE THE OPTIMAL WAYS TO DETERMINE WHETHER A STIMULUS IS GENUINELY INVISIBLE?

As with any technique used to study subliminal perception, CFS studies that report performance or physiological measures indicative of stimulus processing outside of awareness must demonstrate that the stimuli were genuinely suppressed from awareness. In priming and adaptation paradigms, measures of awareness are assessed independently of the measure of processing outside of awareness (i.e., priming effect and aftereffect). In contrast, b-CFS provides an index of awareness to infer stimulus processing outside of awareness, and so this section does not pertain to the b-CFS paradigm. In establishing the absence of awareness, some researchers advocate subjective measures (e.g., Cheesman and Merikle, 1986) whereas others argue for the use of objective measures (e.g., Holender, 1986) to verify observers' unawareness of stimuli suppressed by CFS.

A very popular way of obtaining a subjective measure of awareness in the context of CFS experiments is to ask participants to report any occasion when they perceive another image besides the CFS suppressor. These subjective reports are then used to discard trials where suppression fails (e.g., Kanai et al., 2006; Maruya et al., 2008). Rather than relying on binary judgments of visibility ("yes" versus "no"), there are other, more nuanced ways to cull visible from invisible trials (Sandberg et al., 2010; see Hesselmann, 2013 for review). For instance, observers can rate the quality of their visual experience on a graded scale, such as the perceptual awareness scale (PAS), which includes multiple response options ranging from "no visual experience at all" on one extreme, to "a clear and complete visual experience" on the other (Ramsoy and Overgaard, 2004; see Ludwig et al., 2013 for a CFS study using PAS). In some approaches, reports of subjective experience are supplemented by asking observers to provide confidence ratings of these reports (e.g., Cheesman and Merikle, 1986; Kunimoto et al., 2001). For instance, in one recently introduced form of confidence rating termed post-decision wagering, observers' confidence levels are represented by the amount of money they are willing to bet on the accuracy of their subjective judgments (Persaud et al., 2007). The method should in principle motivate people both to respond in a bias-free manner and to accurately express their confidence level (Persaud et al., 2007; Schurger and Sher, 2008; but see Clifford et al., 2008). Another approach to investigating awareness using confidence ratings aims to characterize the nature of invisibility on trials where observers report seeing no stimulus, by combining confidence ratings on these trials with signal detection theory (Kanai et al., 2010). Only a few studies have applied confidence rating methods to study stimulus analysis during CFS (Bahrami et al., 2008; Sterzer et al., 2008; Raio et al., 2012).

In other published studies, a 2-alternative categorization task has been used to infer the extent to which an observer is aware of a stimulus viewed together with CFS. In two versions of this approach, observers are instructed to either classify the suppressed stimulus into one of two object categories (e.g., tool versus animal; e.g., Almeida et al., 2008; Arnold et al., 2008; Sterzer et al., 2008; Kaunitz et al., 2011b; Raio et al., 2012) or to discriminate the suppressed stimulus from a grid-scrambled version of that stimulus (Fang and He, 2005; Jiang and He, 2006; Jiang et al., 2006, 2009).

Because such tasks require the observer to make a report following CFS presentation, and because many paradigms also involve another behavioral report at that time, these categorization tasks are often implemented in a separate "control" experiment rather than as part of the main experiment, to avoid dual task demands. If performance is not significantly different from chance in the control experiment, investigators conclude that observers were also unaware of the stimuli presented under CFS during the condition of interest.

Potential concerns

Regardless how awareness is assessed when using CFS, there are several considerations to keep in mind. A concern that can arise in the context of subjective awareness measures is that of decision criterion. Specifically, when asking an observer whether he or she perceives a stimulus, a negative response may reflect a conservative criterion rather than lack of awareness of the stimulus (Eriksen, 1960; Holender, 1986). Although this point applies generally to experiments that measure awareness subjectively, it may be particularly pressing in the case of CFS experiments, given that a stimulus pitted against a dynamic CFS display may partially break suppression but rarely overcomes suppression *completely* such that it achieves exclusive dominance. There exists, in other words, a potentially confusing "gray zone" between seeing nothing and, then, experiencing a clean break from suppression. In line with this notion, accruing evidence demonstrates that visual awareness of complex stimuli does, indeed, vary in a graded fashion, both under visual masking (e.g., Overgaard et al., 2006; Seth et al., 2008; Sandberg et al., 2010) and under CFS (Kang et al., 2011; Mudrik et al., 2013).

The possibility of partial visibility during CFS is an important concern in the context of dichotomous subjective report tasks, given that partially visible stimuli that may not elicit a "yes" response in such a task, are likely to nevertheless affect experimental measures. Visual masking studies have shown that the strength of semantic priming correlates with the degree of perception of prime stimuli (e.g., Purcell et al., 1983; Kouider and Dupoux, 2004; Nolan and Caramazza, 2013; review by Kouider and Dehaene, 2007; see also Kouider et al., 2010). To give an example, Kouider and Dupoux (2004) assessed observers' awareness using tasks that tapped into different stages of stimulus processing and observed semantic priming by partially visible words in which observers could accurately discriminate letters yet without recognizing the words as a whole. When observers could neither recognize the words nor discriminate letters, indicating that the words were fully masked, semantic priming was completely abolished.

Objective measures of awareness, in turn, are not free from drawbacks either. Both objective and subjective measures have been critiqued on statistical grounds (Rouder et al., 2007; review by Hesselmann, 2013). Specifically, experimenters who use a yes–no, detection, or discrimination task as their index of awareness may find no significant difference between an observer's objective performance and chance level performance, and then may falsely accept the null hypothesis that observers' performance is equivalent to chance levels, when in reality the experiment is underpowered to detect a reliable difference (Altman and Bland, 1995). Second, whereas the first point suggests that objective measures can be overly liberal in identifying situations as lacking awareness, objective measures have also been argued to be overly conservative. That is, above-chance performance on discrimination tasks could in some cases be attributed to influences that are not accompanied by phenomenal experience, and that may therefore be classified as outside of awareness (Cheesman and Merikle, 1986; Merikle and Daneman, 1998). In such cases there is, therefore, a dissociation between subjective and objective measures of awareness (Stoerig and Cowey, 1997; Kanai et al., 2010). As we will discuss below, this is certainly not the only dissociation between different measures of awareness.

Several additional concerns arise from the fact, mentioned above, that performance levels on the objective task are usually assessed in a control experiment separately from the main experiment. During such a control experiment, the observer is typically instructed to perform a task on a suppressed stimulus across consecutive trials and in the absence of feedback. If CFS is indeed successful at effectively suppressing the stimulus on a majority of the trials, the observer will fail to detect the stimulus over and over again, and there is evidence that this can lead to an underestimation of the observer's true performance levels. For example, one study compared detection of a masked stimulus under two conditions (Pratte and Rouder, 2009; see also Lin and Murray, 2014). One condition consisted exclusively of trials involving this masked stimulus, whereas the other condition also included trials where the stimulus was perceptually visible. In this second condition, observers could reliably detect masked stimuli, but in the first condition, detection performance was at chance level for those same stimuli, arguably because an inability to detect the stimulus on a large proportion of the trials caused inattention or lack of motivation. Similar effects of impaired performance have been observed in visual search experiments where only small a minority of trials contains an actual target (Wolfe et al., 2007).

Aside from this issue of inattention or lack of motivation, two other factors can limit the extent to which awareness measures obtained in a control experiment may not generalize to the main experiment. First, given that the two experiments typically involve different behavioral tasks, observers' strategies are likely to differ in time, potentially leading to differences in awareness (Reingold and Merikle, 1988). Second, perceptual sensitivity and response criteria may vary over time due to adaptation, fatigue or training, disqualifying any techniques that do not allow one to separate this variation from the measure of interest (e.g., Purcell et al., 1983). We should add that these concerns about testing for awareness outside of the main experiment apply with equal force to situations in which awareness measures are obtained from observers different from those tested in the main experiment (Bahrami et al., 2010; Xu et al., 2011; Troiani and Schultz, 2013). Indeed, we see no justification for doing this. The strength of interocular suppression differs considerably among observers; a CFS mask of given contrast may render a dichoptically viewed target completely undetectable for one observer, but for another observer this same CFS mask may prove relatively weak in terms of suppressing a target (Yang et al., 2010a; Zadbood et al., 2011). Despite CFS's reputation for producing potent suppression, individual differences do exist and they could substantially impact the influence of other factors modulating awareness.

Our final concern about objective awareness measures during CFS relates to the point we raised above when discussing subjective awareness measures, and the concern centers on the possibility of partial visibility. When sensory signals are weak or degraded but, at minimal, detectable, observers may fail to consciously access information at different levels of processing and thus different representational levels (Kouider and Dupoux, 2004; Kouider et al., 2010). In the context of objective measures, an observer's awareness is commonly indexed by his or her ability to discriminate between two alternatives in a categorization task on the suppressed stimulus. For instance, an observer may be asked to report whether the stimulus is a tool or an animal (Almeida et al., 2008, 2010). Classifying an image into categories such as these plausibly requires more information than does merely detecting the presence of that image. If a stimulus becomes partially visible, therefore, the situation is similar to the one we described above when discussing subjective awareness measures. Specifically, partial visibility may not be sufficient for performing the classification task used to index awareness, but it may nevertheless influence the independent measure (e.g., priming, adaptation) investigated by the study at hand. In support of this notion, Mudrik et al. (2013) demonstrated that a face suppressed with CFS caused priming when using chance performance on a face identification task as the criterion for including data, but this priming disappeared when the authors instead selected data on the basis of a more stringent location discrimination task.

We will conclude this section with the general note that there is probably no single, foolproof index of awareness. For instance, in the case of "blindsight" subjective and objective measures of awareness conflict with one another. Here cortically lesioned patients deny having any subjective awareness of visual stimuli but can successfully perform objective tasks on those stimuli (e.g., Sahraie et al., 1997; Stoerig and Cowey, 1997; de Gelder et al., 2008). There is evidence for similar dissociations in healthy individuals as well (Kolb and Braun, 1995; Lau and Passingham, 2006). Objective and subjective measures of awareness are not only dissociable at the behavioral level, as Hesselmann et al. (2011) have demonstrated. These authors employed functional magnetic resonance imaging (fMRI) while observers made objective and subjective reports of stimuli suppressed with CFS. Areas beyond early visual cortex were strongly responsive to trials in which observers subjectively reported seeing the "suppressed" stimulus, whereas objective performance on a location discrimination task was correlated with multivariate pattern classification performance using responses from early visual areas.

Recommendations

Based on the considerations detailed above, we come to the following suggestions for a "best practice" approach to measuring the degree of awareness of the suppressed stimulus in CFS experiments.

It should be clear from the above that each awareness measure has its own shortcomings, and also that different awareness measures plausibly index different stages of awareness. This leads to two recommendations. First, it is reasonable to employ multiple measures of awareness side by side, to obtain a more complete assessment of observers' perceptual state under CFS (Sterzer et al., 2008; Kang et al., 2011; Kaunitz et al., 2011b; Yokoyama et al., 2013). Second, it is advisable to be cautious in generalizing findings obtained using one criterion of unawareness, to situations that employ other measures.

Emerging from the considerations raised in this section is a common theme: the transition from complete awareness to unawareness is not abrupt but, instead, unfolds in a graded fashion. With regard to subjective measures of awareness, this means that it is advisable to use report scales with multiple levels, rather than dichotomous ones, to obtain more certainty that awareness was, in fact, lacking in conditions labeled as "unaware." To illustrate this point, studies by Overgaard et al. (2013) have shown that subliminal perceptual effects using a dichotomous measure were no longer observed when executing the same experimental paradigm with the PAS graded report scale. With regard to objective measures, the graded nature of awareness during CFS means that asking observers to cast a verdict about relatively complex stimulus aspects (e.g., semantic category) invites the possibility of overlooking their awareness of basic stimulus features insufficient to perform that task. In other words, it is preferable to ask observers to perform a task on basic stimulus features, instead.

We mentioned the statistical concern that has been raised with regard to objective awareness measures, of falsely accepting the null hypothesis when objective performance does not significantly differ from chance. When aiming to substantiate an unawareness claim using objective measures, it would be a good idea to perform some type of power analysis to minimize a Type II error. For instance, one can use a method involving equivalence confidence intervals (Berger and Hsu, 1996; Overgaard et al., 2013), where one identifies the range of potential values of the dependent variable that would be statistically indistinguishable from chance performance, and then evaluates whether both the lower and upper confidence intervals around the observed variable lie within this range.

As a final recommendation, we pointed out concerns that arise when measuring awareness in an experiment separate from the main one, and the best way to sidestep those concerns is to include the awareness condition within the main experiment. A good example of such an approach was offered by Faivre et al. (2012). Within a single experiment, these authors randomly intermixed trials that required an awareness judgment and ones where the main task was required. Observers were not informed until the end of a trial which kind of trial it was, thus guaranteeing a similar attitude in terms of attention and motivation across both trial types. In situations where it is infeasible to obtain visibility measures within the main experiment, it is useful to at least employ a maximally similar paradigm and task set across both experiments (Reingold and Merikle, 1988) and, ideally, to assess awareness both prior to the main experiment and afterward (e.g., see Jiang and He, 2006; Kang et al., 2011).

WHAT ARE EFFECTIVE METHODS FOR GAGING THE SPECIFICITY AND STRENGTH OF STIMULUS PROCESSING OUTSIDE OF AWARENESS?

A common approach when investigating stimulus processing outside of awareness with CFS is to contrast a given measure in the presence of interocular suppression against that measure in absence of interocular suppression. In priming and adaptation paradigms, these measures tend to map onto conditions where stimuli are visible or invisible owing to CFS. In b-CFS, these measures are typically represented by conditions in which stimuli gradually become visible as a result of either emergence from suppression or some type of stimulus manipulation such as contrast ramping. The comparison of stimulus-driven effects in the presence and absence of interocular suppression allows investigators to index the relative strength and specificity of stimulus processes engaged without an observer's awareness. Take binocular rivalry, for instance, where one can directly compare a stimulus-driven effect when that stimulus is perceptually dominant as opposed to when it is suppressed during rivalry while all other aspects of the stimuli and procedures remain unchanged. This particular approach of holding all conditions identical with the sole exception of an observer's awareness is rather difficult when using CFS, because stimuli are so infrequently and incompletely perceived in the presence of a potent CFS mask. Thus, here CFS's extreme effectiveness for rendering stimuli invisible becomes, paradoxically, a potential drawback. Indeed, this may explain why so many CFS studies that use a priming paradigm choose not to include a visible condition at all: priming effects known to exist based on previous research using visible stimuli were only assessed using prime stimuli rendered invisible by CFS (Almeida et al., 2008, 2010, 2013; Anderson et al., 2012; Faivre et al., 2012; Sakuraba et al., 2012; Zabelina et al., 2013). In these studies, evidence for priming despite CFS is revealing, particularly when the strength of these subliminal priming effects varies across stimulus categories (e.g., tools versus faces). Still, it remains unclear whether priming without awareness is different in magnitude relative to priming with visible stimuli.

Many other CFS studies with priming and adaptation paradigms do include a no-suppression condition, but the potency of CFS often forces researchers to specifically design that condition rather than simply wait for the target stimulus to break through suppression and become visible (for exceptions see Adams et al., 2010; Stein and Sterzer, 2011; Stein et al., 2012a). Next we turn to such CFS studies that do include a no-suppression condition. We will dedicate a separate section of this discussion to paradigms that involve the target stimulus b-CFS, because the choice of the no-suppression condition turns out to be particularly important in those paradigms.

General concerns regarding no-suppression conditions in CFS paradigms

For the no-suppression condition of many physiological and behavioral studies, the CFS mask was simply removed altogether, thereby leaving the monocular stimulus viewed by the other eye easily visible (e.g., Kanai et al., 2006; Yang et al., 2010b; Amihai et al., 2011; Sweeny et al., 2011; Sklar et al., 2012). One potential drawback to this kind of monocular condition is that measures of stimulus-driven effects with the monocularly visible stimulus may be inflated, since removing the CFS mask may also eliminate a large source of external noise. Moreover, removal of the CFS mask may well influence the extent to which contrast normalization influences the effective contrast of the combined left- and right-eye neural signals independent of interocular suppression (e.g., Ding and Sperling, 2006; Said and Heeger, 2013). Consistent with these concerns, some pivotal conclusions based on fMRI results obtained using CFS in combination with a no-mask comparison condition (Fang and He, 2005; Jiang and He, 2006; Sterzer et al., 2008; Vizueta et al., 2011) were not reached in studies where CFS masks were included and matched across experimental conditions (Hesselmann and Malach, 2011; Hesselmann et al., 2011).

No-suppression conditions in b-CFS paradigms

As briefly discussed above, the b-CFS paradigm, unlike other paradigms used with CFS, aims to infer processing of a target stimulus that is suppressed from awareness, by measuring at which moment this suppression ends and the observer becomes aware of that same stimulus (e.g., Jiang et al., 2007; Stein et al., 2011b). In other words, the paradigm, by design, operates right on the border between awareness and unawareness. The same is not true for paradigms involving, say, adaptation or priming, which index processing outside of awareness in terms of detection or performance in a separate task. Just to review, the logic of the b-CFS paradigm entails comparing the RT at which an initially suppressed target stimulus is first detected as it emerges from CFS. When different classes of stimuli show significantly different detection RTs, one presumes that those stimulus categories were differentially processed while suppressed, with faster RTs implying more robust processing outside of awareness. For instance, emotional faces are detected faster than their neutral counterparts as they emerge from CFS (Yang et al., 2007; Tsuchiya et al., 2009; Gray et al., 2010; Sterzer et al., 2011; Stein and Sterzer, 2012; Stein et al., 2014). However, given the characteristic of the b-CFS paradigm of relying on responses made when the target stimulus is *not* suppressed, one needs to be cautious ascribing RT differences to differences in processing outside of awareness. For instance, RT may also be modulated by factors such as general detection ability, response criteria, and basic visual attributes. Ruling out such alternative explanations means that the choice of no-suppression condition is critical, as detailed below.

Alternative explanations to processing outside of awareness can be rejected by demonstrating that RT differences found between two stimulus conditions using the b-CFS procedure disappear when interocular suppression is removed from the picture. The no-suppression condition that is required to demonstrate this should ideally engage all the processes that occur in the invisible condition, with the exception of those that render stimuli invisible (Stein et al., 2011b). In one popular no-suppression condition, the target stimulus is blended into the CFS mask itself so that both target and CFS mask are seen by the same eye, rather than having the target imaged in the eye not viewing the CFS mask, as in the invisible condition (e.g., Costello et al., 2009; Yang and Yeh, 2010; Mudrik et al., 2011; Stein and Sterzer, 2012; Stewart et al., 2012). The blending is implemented so that the target stimulus gradually emerges within the CFS mask during the trial, to perceptually mimic that stimulus emerging from suppression (but see Stein et al., 2011b). As we will discuss next, this approach comes with several subtleties and potential pitfalls.

A primary concern with this kind of "blended" condition is that the resulting RT distribution is almost always significantly different from the RT distribution found for the invisible condition. Most notably, in the no-suppression condition RTs are typically faster and less variable than they are in the invisible condition. The reduced variability, in particular, can be a cause for concern. For instance, a small RT range suggests that the target stimuli may be transitioning from unnoticeable to noticeable rather abruptly. As a result, even if observers do reach decisions about the presence of different stimulus categories at different rates in the blended condition, those differences may be obscured by floor effects that mask decisional influences (e.g., response criterion), which are more evident in the longer RTs measured in the invisible condition.

Another aspect of the relatively small RT variability in the no-suppression condition is related to the fact that the ramping rate typically remains fixed across trials. This constant rate means that observers can develop strong expectancy effects for this condition, effects that are precluded in the invisible conditions by the temporal uncertainty engendered by the more variable durations of suppression. Any differences in expectation between the no-suppression condition and the invisible condition may also lead to differences in observer's response strategies, and these differences are further exacerbated when no-suppression and invisible trials are presented in separate blocks, as often done in CFS studies (Stein et al., 2011b).

Recommendations

For certain CFS designs involving measures such as adaptation and priming, the concerns expressed above make it unwise to compare CFS conditions to conditions without any mask whatsoever. If the CFS masks are truly potent, only a small percentage of trials will fail to produce reliable suppression. It is then possible, with some adaptation paradigms, to compare trials with CFS masks in which suppression succeeded to those in which suppression failed (Adams et al., 2010; Stein and Sterzer, 2011; Stein et al., 2012a). One potential drawback is that it may be laborious to acquire a sufficient number of no-suppression trials. Alternatively, one should try to tone down the CFS mask to allow periods where the target stimulus becomes unequivocally visible. Then, periods of suppression and periods of visibility can be compared, all in the presence of a CFS mask. Some studies have taken steps in this direction, and measured the stimulus conditions that produced reliable suppression for each participant, prior to the main task. In doing so, those studies were able to distinguish stimulus conditions (e.g., contrast values) that different levels of stimulus awareness in the presence of the CFS mask (e.g., Tsuchiya and Koch, 2005; Hesselmann et al., 2011; Kang et al., 2011; Kaunitz et al., 2011b). While more time consuming, measuring CFS under these graded visibility conditions provides a more complete picture of the impact of CFS and visibility. Moreover, conditions with different degrees of visibility in this design may also be more comparable in terms of detectability and attentional engagement.

As for the b-CFS paradigm, there are several improvements in the no-suppression condition that could be implemented. To minimize differences in RT distributions across no-suppression and invisible conditions, the rate at which a stimulus increases in luminance or contrast during a no-suppression trial can be varied to produce RT distributions similar to those measured in the invisible condition (e.g., Stein et al., 2011b, 2012b). After successfully matching RT distributions across conditions with this and related methods, Stein et al. (2011b) found that one differential stimulus effect – the face inversion effect – produced under the invisible condition was observed in the no-suppression condition as well.

To circumvent effects attributed to differences in anticipation and response strategies, it is advisable for no-suppression and invisible trials to be randomly intermixed and, when possible, for response accuracy to be measured rather than RT (Stein et al., 2011b). In fact, this suggestion is applicable to all techniques using CFS. In addition to intermixing no-suppression and invisible trials, varying stimulus onset in both no-suppression and invisible conditions can further reduce differences in temporal uncertainty and minimize anticipation effects in no-suppression trials (Sterzer et al., 2011; Stein and Sterzer, 2012; Gayet et al., 2013). Explicitly modeling response bias or decision criterion (e.g., diffusion models by Smith and Ratcliff, 2004) can at least dissociate RT effects driven by bias in stimulus processing from those driven by more post-perceptual, cognitive (e.g., decision making) processes.

Putting aside, for now, the methodological challenges associated with designing a no-suppression condition for b-CFS, we would like to conclude with a conceptual point. Many studies using b-CFS have now reported stimulus factors that influence the time it takes to report an initially suppressed stimulus. Indeed, such effects have been reported for a broad range of stimulus categories, including words, scenes and faces. True to the logic of no-suppression conditions outlined above, these same studies did not find the same effects on RT when the stimuli were not suppressed, indicating the specific involvement of processes outside of awareness. This remarkable situation raises the question why preferential processing should occur only in the absence of awareness, and why the same mechanisms that affect processing outside of awareness would not influence conscious processing as well. One possibility is that similar influences do affect conscious processing as well, but that these influences can remain undetected for methodological reasons such as the ones outlined above. For instance, early studies have reported shorter RTs for upright faces than for inverted faces during b-CFS but not during visible control conditions, yet more recent work has shown similar effects for visible conditions as well (Stein et al., 2011b). The more fundamental question, however, is this: what kind of processes are we left with when comparing a b-CFS condition with an ideal control condition that is matched in everything but interocular suppression?

As a final methodological suggestion for all CFS paradigms we would like to point to an approach in the literature that has not yet been used in combination with CFS, but whose properties may enable this approach to circumvent some concerns associated with no-suppression conditions. This type of approach, traditionally known as the process-dissociation method, capitalizes on experimental measures that differ qualitatively in awareness (Marcel, 1983; Cheesman and Merikle, 1986; Jacoby, 1991). This relies on the notion that awareness allows observers to intentionally act on information provided by the stimulus, yet that the absence of awareness leads to more automatic reactions to stimulus information that observers cannot intentionally control (Merikle et al., 2001). In a classic example (Debner and Jacoby, 1994; Merikle et al., 1995), an image of a word is perceptually masked and then followed by an image containing the first three letters of that same word. Observers' instructions are to complete the word stem with the first word that came to mind excluding the word that was previously presented. If the previous word was effectively masked, observers are more likely to recall that word when filling in the word stem (i.e., priming effect). However, if the word was visible to observers, they should be able to prevent themselves from using that word. While some concerns have been raised with this particular example (e.g., Fisk and Haase, 2007), there are several other circumstances that can generate qualitatively different effects based on stimulus visibility (e.g., Murphy and Zajonc, 1993; Merikle and Joordens, 1997).

WHAT ARE FACTORS THAT INFLUENCE THE ROBUSTNESS OF STIMULUS-DRIVEN EFFECTS UNDER CFS?

Attention

While the relationship between attention and awareness remains controversial, there is growing consensus that that attention and awareness can to some extent be dissociated (reviews by Koch and Tsuchiya, 2007; van Boxtel et al., 2010a; but Cohen et al., 2012). For instance, lines of research that we will discuss below, suggest that (1) attention can be involuntarily drawn to the location of a stimulus suppressed by CFS, and (2) that attention voluntarily directed toward the location or features of a suppressed stimulus can significantly diminish the extent to which processing of that stimulus is impacted by CFS suppression. While both these notions indicate that CFS suppression and inattention can be separated, the second notion suggests something else as well. Specifically, under the reasonable assumption that observers in standard CFS designs are inclined to pay less attention to the location and features of a target stimulus once they can no longer see the stimulus due to suppression, this second notion leads us to ask whether the reduction in neural processing that is often observed for a suppressed stimulus may, in part, be due to lack of attention to that stimulus. Incidentally, a related issue has been the center of a long-standing debate involving affective priming by stimuli rendered invisible using backward masking (reviews by Pessoa, 2005; Bishop, 2008). Early studies reported subliminal priming effects with and neural responses to affective stimuli rendered invisible with backward masking, pointing to affective processing outside of awareness (e.g., Morris et al., 1998; Whalen et al., 2004). However, recent studies have demonstrated that these effects disappear when attention is sufficiently allocated away from affective stimuli, suggesting that affective processing outside of awareness is conditional upon attention mechanisms (e.g., Phillips et al., 2004; Kouider et al., 2009). In the following section, we will discuss studies of attention manipulations during CFS, as well as their relevance for work examining visual processing under CFS suppression.

First, attention can be involuntarily drawn to the location of a stimulus suppressed by CFS. Specifically, certain categories of stimuli, such as arousing images (Jiang et al., 2006) and emotional facial expressions (Yang et al., 2011), have been shown to attract observers' attention toward the location of those stimuli, even when they are suppressed from awareness with CFS. As a consequence, these invisible stimuli either facilitate or hinder observers' responses to subsequent visible stimuli, which are presented in corresponding or opposing spatial locations. In a related finding, a search task involving a target that was suppressed using CFS revealed that the eyes fixated longer on the location of the target, even though it remained unperceived (Rothkirch et al., 2012). There is also evidence that stimuli such as suppressed faces with averted gaze can cue observers' endogenous spatial attention (Xu et al., 2011). Interestingly, similar findings have not been reported with binocular rivalry, as suppressed visual cues failed to influence observers' spatial attention in a related design (Schall et al., 1993).

Second, attention voluntarily directed to an invisible stimulus can strongly increase the extent to which that stimulus is processed outside of awareness. Specifically, when an observer's spatial or feature-based attention is purposely directed at an invisible stimulus, the effective strength of that visual stimulus is enhanced, as evidenced by the stronger visual aftereffects it induces despite its invisibility (Kanai et al., 2006; Shin et al., 2009; Yang et al., 2010b). Conversely, these aftereffects are substantially weakened, if not abolished, if attention is purposely removed from the suppressed stimulus (Bahrami et al., 2008; Shin et al., 2009; Kaunitz et al., 2011a). In other words, directing attention to the location or to the features of an invisible stimulus modulates the degree to which that stimulus is processed outside of awareness. Physiological support for this notion comes from studies showing that attention allocation and attentional load directly modulate fMRI BOLD responses to stimuli suppressed from awareness by CFS (Bahrami et al., 2007; Watanabe et al., 2011; Yuval-Greenberg and Heeger, 2013). One possible role of attention outside of awareness is to temporarily bind the encoded features of an invisible stimulus to create high-level representations that guide behavioral and perceptual processes outside of awareness (Lin and He, 2009).

In summary, attention may modulate the extent of visual processing under suppression, successfully boosting or weakening neural signals arising from the suppressed stimulus. Considering that inattention to a stimulus is a common, but apparently not necessary, concomitant of perceptually suppressing that stimulus, this observation is important for CFS studies that report reduced or abolished stimulus-driven effects under CFS. Rather than concluding that those effects are modulated by awareness alone, one needs to consider the possibility that they are, at least in part, modulated by attention. To give an illustrative example, one topic that calls for such a cautious attitude is the topic of high-level aftereffects induced by stimuli under CFS. Both complex motion aftereffects (Maruya et al., 2008; Kaunitz et al., 2011a) and various face aftereffects (Shin et al., 2009; Yang et al., 2010b; Amihai et al., 2011; Stein and Sterzer, 2011) can be fully erased by CFS suppression of the inducing stimulus, yet this can to some extent be prevented by making sure the observer keeps attending to the location of the suppressed stimulus (Shin et al., 2009; Yang et al., 2010b; Kaunitz et al., 2011a).

Feature-selective suppression

Many studies of binocular rivalry show that interocular suppression adversely impacts visibility for a broad range of stimuli presented under suppression. Nearly all rivalry studies involving detection or discrimination of test probes have shown that an observer's ability to perceive a wide range of visual features is significantly impaired when probes are presented during interocular suppression, including probes that differ greatly from the currently suppressed target (review by Blake, 2001). It was that pattern of results that led to the characterization of interocular rivalry suppression as non-selective, meaning all classes of visual input are affected, to some extent, when presented under suppression (review by Blake and Logothetis, 2002). This view of suppression dovetails with other findings suggesting that interocular suppression works by reducing effective stimulus contrast or contrast gain of stimulus-evoked responses within early stages of visual processing (Watanabe et al., 2004; Tsuchiya et al., 2006; Yuval-Greenberg and Heeger, 2013). However, this is only half of the story, for there is also evidence for an additional selective component to interocular suppression (Stuit et al., 2009). In the following paragraphs, we review evidence for selectivity obtained using the CFS technique to induce interocular suppression.

Several lines of evidence suggest that processing of some classes of stimuli is less adversely impacted by suppression than is processing of others when CFS is used to induce interocular suppression. For instance, neural processing of objects that fall within categories such as tools and emotional faces appears less susceptible to CFS than is neural processing of stimuli in animal, vehicle, and neutral face categories, as evidenced by the stronger stimulus-induced effects produced by tools and emotional faces under suppression. In this sense, interocular suppression produced by CFS selectively attenuates or abolishes certain signals while leaving others to be potentially encoded during suppression. However, the underlying mechanism for such selective suppression is unclear. Lin and He (2009) proposed a framework in which some critical stimulus features can be registered under CFS, with the degree to which this happens dependent on the type of visual input. Specifically, suppression, in this view, is strongest within functionally specialized areas that comprise the ventral visual pathway, areas in which activity is thought to correlate strongly with object representations (e.g., Rees et al., 2002). In contrast, areas that are relatively unperturbed by CFS may be those comprising the dorsal visual pathway (Fang and He, 2005), as well as the subcortical pathways, presumably more primitive neural circuitry in evolutionary terms and responsible for registering ecologically relevant information including affective content (Morris et al., 1998; Jiang and He, 2006). Lin and He's view is consistent with popular theories supporting the functional significance of dorsal visual and subcortical affective pathways in guiding behavior outside of awareness (e.g., Goodale et al., 1991; Ohman and Mineka, 2001). At the same time, however, evidence consistent with this dorsal/ventral distinction has been challenged by several recent studies demonstrating the importance of feature-based encoding during CFS. These studies are discussed below.

The apparent dissociation in dorsal and ventral stream processing under CFS is primarily supported by reports of object-selective processing of tool images, which are presumably registered within the dorsal stream (Fang and He, 2005; Almeida et al., 2008, 2010). Almeida et al. (2008, 2010) first showed category-related priming effects that were specific to images of tools. However, those investigators did not take into account that, unlike other object categories tested (i.e., animals), tools tend to be elongated in shape, and Sakuraba et al. (2012) later demonstrated that this may be an important factor. Specifically, these latter authors argued that tool-selective priming with CFS was more likely attributable to the encoding of object shape rather than object category, based on their finding that elongated non-tool objects elicited equivalent priming effects whereas non-elongated tools failed to produce any priming (see also Kaunitz et al., 2011b). In addition, physiological evidence for preferential encoding of tools in dorsal areas under CFS (Fang and He, 2005) has not been replicated when CFS displays were presented in both visible and invisible conditions (Hesselmann and Malach, 2011; Hesselmann et al., 2011). Exclusion of the CFS mask in the visible condition may make it difficult to dissociate responses linked to differences in stimulus awareness and those related to discrepancies in stimulus conditions.

The subcortical hypothesis for emotion processing posits that threat-related stimuli are prioritized during stimulus processing that may occur pre-attentively and outside of awareness (review by Phelps and LeDoux, 2005). This theory has been supported by CFS studies demonstrating that fearful face stimuli evoke greater neural responses and break suppression faster than other emotional and neutral face stimuli during CFS (Jiang and He, 2006; Yang et al., 2007; Jiang et al., 2009; Sterzer et al., 2011; Gray et al., 2013; Troiani and Schultz, 2013; Stein et al., 2014). However, a series of recent behavioral studies have shown that this advantage in breaking suppression may not be attributed to the emotional content of fearful faces and may not specifically involve the subcortical pathway. For instance, Gray et al. (2013) demonstrated a similar advantage in breaking suppression for face stimuli that were identical in several low-level visual properties as fearful faces (i.e., spatial frequency, contrast) but were not explicitly or implicitly recognized as fearful in expression. This study thus suggests that the rapid detection of fearful faces may be attributed to properties other than emotional content. In addition, Stein et al. (2014) showed that this fear-based advantage is modulated by differences in high rather than low spatial frequency content across emotional expressions (see also Stein and Sterzer, 2012), which is consistent with a recent study showing that high spatial frequency content is less susceptible to CFS suppression than low spatial frequency content (Yang and Blake, 2012). The Stein et al. (2014) study does not implicate the subcortical pathway since it is thought that this route predominantly conveys coarse low spatial frequency information of threat-related stimuli to the amygdala (Vuilleumier et al., 2003). An additional piece of evidence against the involvement of the amygdala is that patients with bilateral or unilateral lesions to the amygdala show an intact fearful face advantage during CFS (Tsuchiya et al., 2009; Yang et al., 2012; see also Willenbockel et al., 2012).

In summary, differential processing of low-level features likely played a larger role than originally anticipated in several studies using CFS, contributing to the impression that particular routes of visual processing were relatively unaffected by CFS.

Differential suppression of low-level features. Several studies mentioned above underscore the influence of low-level stimulus properties in stimulus-driven effects obtained under CFS suppression. In this context it is important to note that interocular suppression may differentially affect the encoding of different low-level features. Specifically, studies using binocular rivalry (e.g., Yang et al., 1992; Alais and Parker, 2006; Alais and Melcher, 2007), dichoptic masking (e.g., Baker and Meese, 2007) and more recently CFS (Hong and Blake, 2009; Zadbood et al., 2011; Yang and Blake, 2012) have demonstrated that stimulus features most strongly suppressed are those that are shared with the stimulus that induces suppression, or the "suppressor." Recent work shows that this general pattern also applies to the Mondrian-like CFS display that was introduced by Tsuchiya and Koch (2005), and that is the most popular version of CFS display currently in use. Yang and Blake (2012) demonstrated that the features most strongly suppressed by Mondrian patterns are low spatial frequencies and cardinal orientations, which also happen to be the most prominent features of the Mondrian patterns themselves (see also Tsuchiya and Koch, 2005). Furthermore, altering the spatiotemporal properties of the Mondrian patterns also altered the pattern of suppression, such that stimulus features shared by the suppressor were nearly always the ones most strongly suppressed. Stein et al. (2014) found a similar pattern of results with face stimuli and CFS patterns that were varied in spatial frequency content. These investigators also examined suppression with CFS displays that were equivalent in energy across low and high spatial frequency bands. However, suppression remained biased toward low spatial frequency faces even with these filtered displays, and this may be partly attributable to the temporal structure of CFS displays (Yang and Blake, 2012). Other characteristics of CFS using Mondrian displays, include differential suppression of chromatic and achromatic content (Hong and Blake, 2009) and differential suppression of temporal and form information (Zadbood et al., 2011). Finally, the pattern of feature-selective suppression demonstrated with the Mondrian display may generalize to other CFS displays previously used, since Yang and Blake showed that these tend to have spectral profiles similar to that of the Mondrian display (Supplementary Figure 1 in Yang and Blake, 2012). It may be this particular spectral profile that leads to the potent suppression evoked by CFS.

Considered together, the processing of a stimulus under CFS will be adversely impacted in general (non-selective suppression) but to an extent that depends on the similarity between that stimulus and the stimulus doing the suppression [feature-selective suppression, similar to that described by Stuit et al. (2009), for conventional binocular rivalry]. This is important for at least two reasons. First, weakly suppressed stimulus features are more likely to be visible to observers but experimenters may fail to detect observers' awareness of them (see section above). As a result, visible stimulus fragments may modulate stimulus-driven effects that are mistakenly attributed to processing outside of awareness. Second, even for fully suppressed stimuli, information processing under CFS is determined, in part, by differences in the extent to which basic visual features are impacted by CFS. These two notions are important for studies in which stimulus-driven effects are attributed to encoding of high-level, semantic information during CFS (review by Lin and He, 2009), and in particular when experimenters use stimuli whose similarity in basic visual features is larger within the same semantic category than it is between categories (Kouider and Dehaene, 2007). Especially when selective feature encoding is paired with factors such as small stimulus sets and high rates of stimulus repetition across trials, feature-selective suppression may play a large role in stimulus-driven effects under CFS. In sum, the differential impact of CFS on low-level stimulus features must be considered as an alternative explanation for findings that might otherwise be attributed to high-level visual processing under CFS. Conversely, one may get some idea of the extent to which various later stages of analysis could still function under CFS by considering the extent to which CFS selectively inhibits the basic visual signals that provide input to those stages.

General recommendations

We recommend that observers' attentional state be carefully controlled during tasks involving CFS. For example, attention can be cued to the location of the suppressed stimulus to maximize visual processing under suppression. Importantly, when select visual processes are hypothesized as being engaged automatically or in the absence of awareness, it should be made explicit whether these processes are also independent of observers' attentional engagement. One common approach to examining the role of attention in visual processing outside of awareness is to compare the strength of stimulus-driven effects under conditions where attention is directed toward versus away from suppressed target stimuli.

To avoid the potential effects of feature-selective suppression described above, we recommend that experimenters select target images that are similar in spatial composition (e.g., shape, size) within and across stimulus categories or, better yet, create images comprised of different phase spectra but identical amplitude spectra using image processing techniques. Secondly, certain spatial properties can be normalized across stimuli such as spatial frequency amplitude, contrast, mean luminance, orientation content, shape, and size. Finally, we recommend that experimenters use CFS displays that are similar in spatial profile as the target stimuli to be suppressed, in order to maximize suppression of all components of the target stimulus. Alternatively, one can manipulate stimuli to have similar spatial profiles as the CFS display without necessarily altering stimulus recognition. Based on previous studies (Hong and Blake, 2009; Yang and Blake, 2012), achromatic Mondrian displays may prove to be most effective at suppressing static, achromatic images composed of low spatial frequency, cardinally oriented features. Considering that visible or weakly suppressed features may still occur, one further measure one can take is to use large stimulus sets or to replicate findings with multiple stimulus sets, to minimize learned associations or effects of stimulus repetition across trials.

CONCLUSION

Those of us interested in visual processing outside of awareness have at our disposal an impressive array of tools for manipulating visual awareness. Among those tools, CFS is particularly appealing, since it offers several advantages compared to other techniques at rendering stimuli invisible. Not surprisingly, the technique has caught on within the field, and the volume of results for processing outside of awareness obtained with this technique is already quite substantial despite the technique's appearance on the scene <10 years ago. Surveying studies that have employed CFS, one sees several different ways in which CFS is being exploited, each with its own subtleties that may influence the likelihood of finding evidence for visual processing outside of awareness. Researchers intending to use CFS will learn that multiple factors must be taken into consideration when using this technique; we believe the majority of those considerations can be grouped into four primary questions. In this paper, we have provided recommendations for addressing those questions, and those recommendations are briefly reiterated below.

(1) What are suitable paradigms to use with CFS to study processing outside of awareness?

- Measures of adaptation aftereffects are useful in examining neural processes involved in the encoding of visual attributes of a stimulus.
- Priming paradigms allow researchers to examine processing of physical and conceptual (semantic) characteristics shared by two stimuli.
- The b-CFS paradigm relies on the speed at which stimuli emerge from suppression to infer the relative strength of stimulus processing outside of awareness. This technique has been widely used in examining semantic processes outside of awareness.

(2) What are the optimal ways to determine whether a stimulus is genuinely invisible?

- To obtain a more complete evaluation of observers' perceptual state under CFS with adaptation or priming paradigms, we advise the employment of multiple measures of awareness, which include measures that assess different states of awareness (i.e., objective, subjective) and measures that gage different stages of stimulus analysis.
- We recommend the use of statistical analyses that reduce the likelihood of falsely accepting the null hypothesis that observers' performance on an awareness measure is not significantly different from chance, with the implication that stimuli were sufficiently rendered invisible.
- We urge that awareness measures be implemented *within* the main experiment, and that those measures be administered in ways that recreate, as nearly as possible, the attentional state and response strategies engendered during the main task when the target stimulus is putatively suppressed from awareness by CFS.

(3) What are effective methods for gaging the specificity and strength of stimulus processing outside of awareness?

- Studies should strive to compare stimulus-driven effects found with CFS to those measured without suppression.
- The no-suppression condition(s) should be matched as closely as possible to the invisible condition.
- We recommend that no-suppression and invisible trials be randomly intermixed to minimize potential differences between conditions (i.e., differences such as anticipation and response strategy).
- For the b-CFS procedure, the no-suppression condition should be individually tailored for each participant to produce similar RT distributions in the behavioral task and similar perceptual experiences for the no-suppression and invisible conditions.

(4) What are factors that influence the robustness of stimulus-driven effects under CFS?

- The spatial location of an observer's attentional engagement can modulate visual processing under CFS. Thus:
  - It is advisable to hold an observer's spatial attention constant across trials, particularly directing attention to the location of the stimulus being suppressed so as to maximize the likelihood of stimulus processing under CFS.
  - Researchers should also consider manipulating an observers' spatial attention to test whether stimulus processing is engaged without awareness *and* without attention.
- Low-level features of target stimulus and CFS display can modulate the strength and selectivity of suppression.
  - Target images should be closely matched in spatial composition with one another and with the CFS mask.

In closing, we are excited about the future opportunities for learning more about stimulus processing outside of awareness, and we are confident that CFS can provide one effective means for pursuing that question. Coincidentally, the recent resurgence of interest in processing outside of awareness coincides with the forthcoming one-hundredth anniversary of the publication of one of Sigmund Freud's most famous essays, *The Unconscious* (Freud, 1915). For decades, Freud's ideas have been construed as quaint but outmoded, relying as they did on anecdote and scientifically untestable conjecture. It is fair to say that Freud's ideas about the unconscious provided enjoyable literature but fell outside of the domain of serious psychological science. Ironically, we now find ourselves armed with modern techniques like CFS for probing the unconscious, and there appears to be a growing army of troops enlisting to do just that. Our modest hope is that the concerns about CFS and possible solutions we have voiced in this essay will provide useful guidelines for strengthening the inferential potential of CFS. At the same time, we believe that CFS alone is not going to provide a definitive answer to the question of processing outside of awareness. Instead, we will need to use CFS in conjunction with other techniques for manipulating awareness (Kim and Blake, 2005) to arrive at conclusions about stimulus processing outside of awareness that are not method-specific.

REFERENCES

Adams, W. J., Gray, K., Garner, M., and Graf, E. W. (2010). High-level face adaptation without awareness. *Psychol. Sci.* 21, 205–210. doi: 10.1177/0956797609359508

Alais, D., and Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. *Vision Res.* 47, 269–279. doi: 10.1016/j.visres.2006.09.003

Alais, D., and Parker, A. (2006). Independent binocular rivalry processes for motion and form. *Neuron* 52, 911–920. doi: 10.1016/j.neuron.2006.10.027

Almeida, J., Mahon, B. Z., and Caramazza, A. (2010). The role of the dorsal visual processing stream in tool identification. *Psychol. Sci.* 21, 772–778. doi: 10.1177/0956797610371343

Almeida, J., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proc. Natl. Acad. Sci. U.S.A.* 105, 15214–15218. doi: 10.1073/pnas.0805867105

Almeida, J., Pajtas, P. E., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2013). Affect of the unconscious: visually suppressed angry faces modulate our decisions. *Cogn. Affect. Behav. Neurosci.* 13, 94–101. doi: 10.3758/s13415-012-0133-7

Alpers, G. W., and Gerdes, A. B. M. (2007). Here is looking at you: emotional faces predominate in binocular rivalry. *Emotion* 7, 495–506. doi: 10.1037/1528-3542.7.3.495

Alsius, A., and Munhall, K. G. (2013). Detection of audiovisual speech correspondences without visual awareness. *Psychol. Sci.* 24, 423–431. doi: 10.1177/0956797612457378

Altman, D. G., and Bland, J. M. (1995). Absence of evidence is not evidence of absence. *BMJ* 311:485. doi: 10.1136/bmj.311.7003.485

Amihai, I., Deouell, L., and Bentin, S. (2011). Conscious awareness is necessary for processing race and gender information from faces. *Conscious. Cogn.* 20, 269–279. doi: 10.1016/j.concog.2010.08.004

Anderson, E., Siegel, E., White, D., and Barrett, L. F. (2012). Out of sight but not out of mind: unseen affective faces influence evaluations and social impressions. *Emotion* 12, 1210–1221. doi: 10.1037/a0027514

Arnold, D. H., Law, P., and Wallis, T. S. A. (2008). Binocular switch suppression: a new method for persistently rendering the visible invisible. *Vision Res.* 48, 994–1001. doi: 10.1016/j.visres.2008.01.020

Bahrami, B., Carmel, D., Walsh, V., Rees, G., and Lavie, N. (2008). Unconscious orientation processing depends on perceptual load. *J. Vis.* 8, 12.1–12.10.

Bahrami, B., Lavie, N., and Rees, G. (2007). Attentional load modulates responses of human primary visual cortex to invisible stimuli. *Curr. Biol.* 17, 509–513. doi: 10.1016/j.cub.2007.01.070

Bahrami, B., Vetter, P., Spolaore, E., Pagano, S., Butterworth, B., and Rees, G. (2010). Unconscious numerical priming despite interocular suppression. *Psychol. Sci.* 21, 224–233. doi: 10.1177/0956797609360664

Baker, D. H., and Meese, T. S. (2007). Binocular contrast interactions: dichoptic masking is not a single process. *Vision Res.* 47, 3096–3107. doi: 10.1016/j.visres.2007.08.013

Bannerman, R. L. L., Milders, M., de Gelder, B., and Sahraie, A. (2008). Influence of emotional facial expressions on binocular rivalry. *Ophthalmic Physiol. Opt.* 28, 317–326. doi: 10.1111/j.1475-1313.2008.00568.x

Berger, R. L., and Hsu, J. C. (1996). Bioequivalence trials, intersection-union tests and equivalence confidence sets. *Stat. Sci.* 11, 283–319. doi: 10.1214/ss/1032280304

Bishop, S. J. (2008). Neural mechanisms underlying selective attention to threat. *Ann. N. Y. Acad. Sci.* 1129, 141–152. doi: 10.1196/annals.1417.016

Blake, R. (2001). A primer on binocular rivalry, including current controversies. *Brain Mind* 2, 5–38. doi: 10.1023/A:1017925416289

Blake, R., and He, S. (2005). "Adaptation as a tool for probing the neural correlates of visual awarenss: progress and precautions," in *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision*, eds C. W. G. Clifford and G. Rhodes (Oxford: Oxford University press), 281–307.

Blake, R., and Logothetis, N. K. (2002). Visual competition. *Nat. Rev. Neurosci.* 3, 13–21. doi: 10.1038/nrn701

Blake, R., O'Shea, R. P., and Mueller, T. J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. *Vis. Neurosci.* 8, 469–478. doi: 10.1017/S0952523800004971

Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., and Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 4783–4788. doi: 10.1073/pnas.0509634103

Breese, B. B. (1909). Binocular rivalry. *Psychol. Rev.* 16, 410–415. doi: 10.1037/h0075805

Bridgeman, B. (1992). Conscious vs. unconscious processes: the case of vision. *Theory Psychol.* 2, 73–88. doi: 10.1177/0959354392021004

Carter, O., and Cavanagh, P. (2007). Onset rivalry: brief presentation isolates an early independent phase of perceptual competition. *PLoS ONE* 2:e343. doi: 10.1371/journal.pone.0000343

Cave, C. B., Blake, R., and McNamara, T. P. (1998). Binocular rivalry disrupts visual priming. *Psychol. Sci.* 9, 299–302. doi: 10.1111/1467-9280.00059

Cheesman, J., and Merikle, P. M. (1986). Distinguishing conscious from unconscious perceptual processes. *Can. J. Psychol.* 40, 343–367. doi: 10.1037/h0080103

Chong, S. C., Tadin, D., and Blake, R. (2005). Endogenous attention prolongs dominance durations in binocular rivalry. *J. Vis.* 5, 1004–1012. doi: 10.1167/5.11.6

Clifford, C. W. G., Arabzadeh, E., and Harris, J. A. (2008). Getting technical about awareness. *Trends Cogn. Sci.* 12, 54–58. doi: 10.1016/j.tics.2007.11.009

Cohen, M. A., Cavanagh, P., Chun, M. M., and Nakayama, K. (2012). The attentional requirements of consciousness. *Trends Cogn. Sci.* 16, 411–417. doi: 10.1016/j.tics.2012.06.013

Costello, P., Jiang, Y., Baartman, B., McGlennen, K., and He, S. (2009). Semantic and subword priming during binocular suppression. *Conscious. Cogn.* 18, 375–382. doi: 10.1016/j.concog.2009.02.003

Debner, J. A., and Jacoby, L. L. (1994). Unconscious perception: attention, awareness, and control. *J. Exp. Psychol. Learn. Mem. Cogn.* 20, 304–317. doi: 10.1037/0278-7393.20.2.304

de Gelder, B., Tamietto, M., van Boxtel, G., Goebel, R., Sahraie, A., van den Stock, J., et al. (2008). Intact navigation skills after bilateral loss of striate cortex. *Curr. Biol.* 18, R1128–R1129. doi: 10.1016/j.cub.2008.11.002

de Zilva, D., Vu, L., Newell, B. R., and Pearson, J. (2013). Exposure is not enough: suppressing atimuli from awareness can abolish the mere exposure effect. *PLoS ONE* 8:e77726. doi: 10.1371/journal.pone.0077726

Ding, J., and Sperling, G. (2006). A gain-control theory of binocular combination. *Proc. Natl. Acad. Sci. U.S.A.* 103, 1141–1146. doi: 10.1073/pnas.0509629103

Engel, E. (1956). The rôle content in binocular resolution. *Am. J. Psychol.* 69, 87–91. doi: 10.2307/1418119

Eriksen, C. W. (1960). Discrimination and learning without awareness: a methodological survey and evaluation. *Psychol. Rev.* 67, 279–300. doi: 10.1037/h0041622

Faivre, N., Berthet, V., and Kouider, S. (2012). Nonconscious influences from emotional faces: a comparison of visual crowding, masking, and continuous flash suppression. *Front. Psychol.* 3:129. doi: 10.3389/fpsyg.2012.00129

Fang, F., and He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nat. Neurosci.* 8, 1380–1385. doi: 10.1038/nn1537

Fisk, G. D., and Haase, S. J. (2007). Exclusion failure does not demonstrate unconscious perception. *Am. J. Psychol.* 120, 173–204.

Fox, R., and Herrmann, J. (1967). Stochastic properties of binocular rivalry alternations. *Percept. Psychophys.* 2, 432–436. doi: 10.3758/BF03208783

Freud, S. (1915). "The unconscious," in *The Standard Edition of the Complete Psychological Works of Sigmund Freud*, Vol. 14, ed. J. Strachey (London: Hogarth Press).

Gayet, S., Paffen, C. L. E., and der Stigchel, S. V. (2013). Information matching the content of visual working memory is prioritized for conscious access. *Psychol. Sci.* 24, 2472–2480. doi: 10.1177/0956797613495882

Goodale, M. A., and Milner, A. D. (2004). *Sight Unseen: An Exploration of Conscious and Unconscious Vision.* Oxford: Oxford University press.

Goodale, M. A., Milner, A. D., Jakobson, L. S., and Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature* 349, 154–156. doi: 10.1038/349154a0

Gray, K., Adams, W., and Garner, M. (2010). Preferential processing of fear faces: emotional content vs. low-level visual properties. *J. Vis.* 10:610. doi: 10.1167/10.7.610

Gray, K. L. H., Adams, W. J., Hedger, N., Newton, K. E., and Garner, M. (2013). Faces and awareness: low-level, not emotional factors determine perceptual dominance. *Emotion* 13, 537–544. doi: 10.1037/a0031403

Hesselmann, G. (2013). Dissecting visual awareness with fMRI. *Neuroscientist* 19, 495–508. doi: 10.1177/1073858413485988

Hesselmann, G., Hebart, M., and Malach, R. (2011). Differential BOLD activity associated with subjective and objective reports during 'blindsight' in normal observers. *J. Neurosci.* 31, 12936–12944. doi: 10.1523/JNEUROSCI.1556-11.2011

Hesselmann, G., and Malach, R. (2011). The link between fMRI-BOLD activation and perceptual awareness is 'atream-invariant' in the human visual system. *Cereb. Cortex* 21, 2829–2837. doi: 10.1093/cercor/bhr085

Holender, D. (1986). Semantic activation without conscious identification in dichotic listening, parafoveal vision, and visual masking: a survey and appraisal. *Behav. Brain Sci.* 9, 1–23. doi: 10.1017/S0140525X00021269

Hong, S. W., and Blake, R. (2009). Interocular suppression differentially affects achromatic and chromatic mechanisms. *Attent. Percept. Psychophys.* 71, 403–420. doi: 10.3758/APP.71.2.403

Hugrass, L., and Crewther, D. (2012). Willpower and conscious percept: volitional switching in binocular rivalry. *PLoS ONE* 7:e35963. doi: 10.1371/journal.pone.0035963

Jacoby, L. L. (1991). A process dissociation framework: separating automatic from intentional uses of memory. *J. Mem. Lang.* 30, 513–541. doi: 10.1016/0749-596X(91)90025-F

Jiang, Y., and He, S. (2006). Cortical responses to invisible faces: dissociating subsystems for facial-information processing. *Curr. Biol.* 16, 2023–2029. doi: 10.1016/j.cub.2006.08.084

Jiang, Y., Costello, P., and He, S. (2007). Processing of invisible stimuli: advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychol. Sci.* 18, 349–355. doi: 10.1111/j.1467-9280.2007.01902.x

Jiang, Y., Costello, P., Fang, F., Huang, M., and He, S. (2006). A gender- and sexual orientation-dependent spatial attentional effect of invisible images. *Proc. Natl. Acad. Sci. U.S.A.* 103, 17048–17052. doi: 10.1073/pnas.0605678103

Jiang, Y., Shannon, R. W., Vizueta, N., Bernat, E. M., Patrick, C. J., and He, S. (2009). Dynamics of processing invisible faces in the brain: automatic neural encoding of facial expression information. *Neuroimage* 44, 1171–1177. doi: 10.1016/j.neuroimage.2008.09.038

Kanai, R., Tsuchiya, N., and Verstraten, F. A. J. (2006). The scope and limits of top-down attention in unconscious visual processing. *Curr. Biol.* 16, 2332–2336. doi: 10.1016/j.cub.2006.10.001

Kanai, R., Walsh, V., and Tseng, C. H. (2010). Subjective discriminability of invisibility: a framework for distinguishing perceptual and attentional failures of awareness. *Conscious. Cogn.* 19, 1045–1057. doi: 10.1016/j.concog.2010.06.003

Kang, M.-S., Blake, R., and Woodman, G. F. (2011). Semantic analysis does not occur in the absence of awareness induced by interocular suppression. *J. Neurosci.* 31, 13535–13545. doi: 10.1523/JNEUROSCI.1691-11.2011

Kaunitz, L., Fracasso, A., and Melcher, D. (2011a). Unseen complex motion is modulated by attention and generates a visible aftereffect. *J. Vis.* 11, 1–9. doi: 10.1167/11.13.10

Kaunitz, L., Kamienkowski, J., Olivetti, E., Murphy, B., Avesani, P., and Melcher, D. (2011b). Intercepting the first pass: rapid categorization is suppressed for unseen stimuli. *Front. Psychol.* 2:198. doi: 10.3389/fpsyg.2011.00198

Kim, C. Y., and Blake, R. (2005). Psychophysical magic: rendering the visible 'invisible.' *Trends Cogn. Sci.* 9, 381–388. doi: 10.1016/j.tics.2005.06.012

Koch, C., and Tsuchiya, N. (2007). Attention and consciousness: two distinct brain processes. *Trends Cogn. Sci.* 11, 16–22. doi: 10.1016/j.tics.2006.10.012

Kolb, F. C., and Braun, J. (1995). Blindsight in normal observers. *Nature* 377, 336–338. doi: 10.1038/377336a0

Kouider, S., de Gardelle, V., Sackur, J., and Dupoux, E. (2010). How rich is consciousness? The partial awareness hypothesis. *Trends Cogn. Sci.* 14, 301–307. doi: 10.1016/j.tics.2010.04.006

Kouider, S., and Dehaene, S. (2007). Levels of processing during non-conscious perception: a critical review of visual masking. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 362, 857–875. doi: 10.1098/rstb.2007.2093

Kouider, S., and Dupoux, E. (2004). Partial awareness creates the 'illusion' of subliminal semantic priming. *Psychol. Sci.* 15, 75–81. doi: 10.1111/j.0963-7214.2004.01502001.x

Kouider, S., Eger, E., Dolan, R., and Henson, R. (2009). Activity in face-responsive brain regions is modulated by invisible, attended faces: evidence from masked priming. *Cereb. Cortex* 19, 13–23. doi: 10.1093/cercor/bhn048

Kunimoto, C., Miller, J., and Pashler, H. (2001). Confidence and accuracy of near-threshold discrimination responses. *Conscious. Cogn.* 10, 294–340. doi: 10.1006/ccog.2000.0494

Lack, L. C. (1978). *Selective Attention and the Control of Binocular Rivalry.* New York, NY: Mouton.

Lau, H. C., and Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 18763–18768. doi: 10.1073/pnas.0607716103

Levelt, W. J. M. (1965). *On Binocular Rivalry.* Soesterberg: Institute for perception RVO-TNO.

Ling, S., and Blake, R. (2009). Suppression during binocular rivalry broadens orientation tuning. *Psychol. Sci.* 20, 1348–1355. doi: 10.1111/j.1467-9280.2009.02446.x

Lin, Z., and He, S. (2009). Seeing the invisible: the scope and limits of unconscious processing in binocular rivalry. *Prog. Neurobiol.* 87, 195–211. doi: 10.1016/j.pneurobio.2008.09.002

Lin, Z., and Murray, S. O. (2014). Priming of awareness or how not to measure visual awareness. *J. Vis.* 14:27. doi: 10.1167/14.1.27

Logothetis, N. K., Leopold, D. A., and Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature* 380, 621–624. doi: 10.1038/380621a0

Losciuto, L. A., and Hartley, E. L. (1963). Religious affiliation and open-mindedness in binocular resolution. *Percept. Mot. Skills* 17, 427–430.

Ludwig, K., Sterzer, P., Kathmann, N., Franz, V. H., and Hesselmann, G. (2013). Learning to detect but not to grasp suppressed visual stimuli. *Neuropsychologia* 51, 2930–2938. doi: 10.1016/j.neuropsychologia.2013.09.035

Lupyan, G., and Ward, E. J. (2013). Language can boost otherwise unseen objects into visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* 110, 14196–14201. doi: 10.1073/pnas.1303312110

Marcel, A. J. (1983). Conscious and unconscious perception: an approach to the relations between phenomenal experience and perceptual processes. *Cogn. Psychol.* 15, 238–300. doi: 10.1016/0010-0285(83)90010-5

Maruya, K., Watanabe, H., and Watanabe, M. (2008). Adaptation to invisible motion results in low-level but not high-level aftereffects. *J. Vis.* 8, 7.1–7.11. doi: 10.1167/8.11.7

Meenes, M. (1930). A phenomenological description of retinal rivalry. *Am. J. Psychol.* 42, 260–269. doi: 10.2307/1415275

Meng, M., and Tong, F. (2004). Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *J. Vis.* 4, 539–551. doi: 10.1167/4.7.2

Merikle, P. M., and Daneman, M. (1998). Psychological investigations of unconscious perception. *J. Conscious. Stud.* 5, 5–18.

Merikle, P. M., and Joordens, S. (1997). Parallels between perception without attention and perception without awareness. *Conscious. Cogn.* 6, 219–236. doi: 10.1006/ccog.1997.0310

Merikle, P. M., Joordens, S., and Stolz, J. A. (1995). Measuring the relative magnitude of unconscious influences. *Conscious. Cogn.* 4, 422–439. doi: 10.1006/ccog.1995.1049

Merikle, P. M., Smilek, D., and Eastwood, J. D. (2001). Perception without awareness: perspectives from cognitive psychology. *Cognition* 79, 115–134. doi: 10.1016/S0010-0277(00)00126-8

Mollon, J. (1974). After-effects and the brain. *New Sci.* 21, 479–482.

Morris, J. S., Ohman, A., and Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature* 393, 467–470. doi: 10.1038/30976

Mudrik, L., Breska, A., Lamy, D., and Deouell, L. (2011). Integration without awareness: expanding the limits of unconscious processing. *Psychol. Sci.* 22, 764–770. doi: 10.1177/0956797611408736

Mudrik, L., Gelbard-Sagiv, H., Faivre, N., and Koch, C. (2013). Knowing where without knowing what: partial awareness and high-level processing in continuous flash suppression. *J. Vis.* 13:1103. doi: 10.1167/13.9.1103

Murphy, S. T., and Zajonc, R. B. (1993). Affect, cognition, and awareness: affective priming with optimal and suboptimal stimulus exposures. *J. Pers. Soc. Psychol.* 64, 723–739. doi: 10.1037/0022-3514.64.5.723

Nolan, K. A., and Caramazza, A. (2013). Unconscious perception of meaning: a failure to replicate. *Bull. Psychon. Soc.* 20, 23–26. doi: 10.3758/BF03334791

Ohman, A., and Mineka, S. (2001). Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychol. Rev.* 108, 483–522. doi: 10.1037/0033-295X.108.3.483

Ooi, T. L., and He, Z. J. (1999). Binocular rivalry and visual awareness: the role of attention. *Perception* 28, 551–574. doi: 10.1068/p2923

Overgaard, M., Lindeløv, J., Svejstrup, S., Døssing, M., Hvid, T., Kauffmann, O., et al. (2013). Is conscious stimulus identification dependent on knowledge of the perceptual modality? Testing the 'source misidentification hypothesis.' *Front. Psychol.* 4:116. doi: 10.3389/fpsyg.2013.00116

Overgaard, M., Rote, J., Mouridsen, K., and Ramsøy, T. Z. (2006). Is conscious perception gradual or dichotomous? A comparison of report methodologies during a visual task. *Conscious. Cogn.* 15, 700–708. doi: 10.1016/j.concog.2006.04.002

Persaud, N., McLeod, P., and Cowey, A. (2007). Post-decision wagering objectively measures awareness. *Nat. Neurosci.* 10, 257–261. doi: 10.1038/nn1840

Pessoa, L. (2005). To what extent are emotional visual stimuli processed without attention and awareness? *Curr. Opin. Neurobiol.* 15, 188–196. doi: 10.1016/j.conb.2005.03.002

Phelps, E. A., and LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: from animal models to human behavior. *Neuron* 48, 175–187. doi: 10.1016/j.neuron.2005.09.025

Phillips, M. L., Williams, L. M., Heining, M., Herba, C. M., Russell, T., Andrew, C., et al. (2004). Differential neural responses to overt and covert presentations of facial expressions of fear and disgust. *Neuroimage* 21, 1484–1496. doi: 10.1016/j.neuroimage.2003.12.013

Pratte, M. S., and Rouder, J. N. (2009). A task-difficulty artifact in subliminal priming. *Attent. Percept. Psychophys.* 71, 1276–1283. doi: 10.3758/APP.71.6.1276

Purcell, D. G., Stewart, A. L., and Stanovich, K. E. (1983). Another look at semantic priming without awareness. *Percept. Psychophys.* 34, 65–71. doi: 10.3758/BF03205897

Raio, C. M., Carmel, D., Carrasco, M., and Phelps, E. A. (2012). Nonconscious fear is quickly acquired but swiftly forgotten. *Curr. Biol.* 22, R477–R479. doi: 10.1016/j.cub.2012.04.023

Ramsoy, T. Z., and Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenol. Cogn. Sci.* 3, 1–23. doi: 10.1023/B:PHEN.0000041900.30172.e8

Rees, G., Kreiman, G., and Koch, C. (2002). Neural correlates of consciousness in humans. *Nat. Rev. Neurosci.* 3, 261–270. doi: 10.1038/nrn783

Reingold, E. M., and Merikle, P. M. (1988). Using direct and indirect measures to study perception without awareness. *Percept. Psychophys.* 44, 563–575. doi: 10.3758/BF03207490

Rothkirch, M., Stein, T., Sekutowicz, M., and Sterzer, P. (2012). A direct oculomotor correlate of unconscious visual processing. *Curr. Biol.* 22, R514–R515. doi: 10.1016/j.cub.2012.04.046

Rouder, J. N., Morey, R. D., Speckman, P. L., and Pratte, M. S. (2007). Detecting chance: a solution to the null sensitivity problem in subliminal priming. *Psychon. Bull. Rev.* 14, 597–605. doi: 10.3758/BF03196808

Sahraie, A., Weiskrantz, L., Barbur, J. L., Simmons, A., Williams, S. C., and Brammer, M. J. (1997). Pattern of neuronal activity associated with conscious and unconscious processing of visual signals. *Proc. Natl. Acad. Sci. U.S.A.* 94, 9406–9411. doi: 10.1073/pnas.94.17.9406

Said, C. P., and Heeger, D. J. (2013). A model of binocular rivalry and cross-orientation suppression. *PLoS Comput. Biol.* 9:e1002991. doi: 10.1371/journal.pcbi.1002991

Sakuraba, S., Sakai, S., Yamanaka, M., Yokosawa, K., and Hirayama, K. (2012). Does the human dorsal stream really process a category for tools? *J. Neurosci.* 32, 3949–3953. doi: 10.1523/JNEUROSCI.3973-11.2012

Sandberg, K., Timmermans, B., Overgaard, M., and Cleeremans, A. (2010). Measuring consciousness: is one measure better than the other? *Conscious. Cogn.* 19, 1069–1078. doi: 10.1016/j.concog.2009.12.013

Schall, J. D., Nawrot, M., Blake, R., and Yu, K. (1993). Visually guided attention is neutralized when informative cues are visible but unperceived. *Vision Res.* 33, 2057–2064. doi: 10.1016/0042-6989(93)90004-G

Schurger, A., and Sher, S. (2008). Awareness, loss aversion, and post-decision wagering. *Trends Cogn. Sci.* 12, 209–210. doi: 10.1016/j.tics.2008.02.012

Seth, A. K., Dienes, Z., Cleeremans, A., Overgaard, M., and Pessoa, L. (2008). Measuring consciousness: relating behavioural and neurophysiological approaches. *Trends Cogn. Sci.* 12, 314–321. doi: 10.1016/j.tics.2008.04.008

Shin, K., Stolte, M., and Chong, S. C. (2009). The effect of spatial attention on invisible stimuli. *Attent. Percept. Psychophys.* 71, 1507–1513. doi: 10.3758/APP.71.7.1507

Sklar, A. Y., Levy, N., Goldstein, A., Mandel, R., Maril, A., and Hassin, R. R. (2012). Reading and doing arithmetic nonconsciously. *Proc. Natl. Acad. Sci. U.S.A.* 109, 19614–19619. doi: 10.1073/pnas.1211645109

Smith, P. L., and Ratcliff, R. (2004). Psychology and neurobiology of simple decisions. *Trends Neurosci.* 27, 161–168. doi: 10.1016/j.tins.2004.01.006

Snodgrass, M., Bernat, E., and Shevrin, H. (2004). Unconscious perception: a model-based approach to method and evidence. *Percept. Psychophys.* 66, 846–867. doi: 10.3758/BF03194978

Song, C., and Yao, H. (2009). Duality in binocular rivalry: distinct sensitivity of percept sequence and percept duration to imbalance between monocular stimuli. *PLoS ONE* 4:e6912. doi: 10.1371/journal.pone.0006912

Stein, T., and Sterzer, P. (2011). High-level face shape adaptation depends on visual awareness: evidence from continuous flash suppression. *J. Vis.* 11, 1–14. doi: 10.1167/11.8.5

Stein, T., and Sterzer, P. (2012). Not just another face in the crowd: detecting emotional schematic faces during continuous flash suppression. *Emotion* 12, 988–996. doi: 10.1037/a0026944

Stein, T., Senju, A., Peelen, M. V., and Sterzer, P. (2011a). Eye contact facilitates awareness of faces during interocular suppression. *Cognition* 119, 307–311. doi: 10.1016/j.cognition.2011.01.008

Stein, T., Hebart, M. N., and Sterzer, P. (2011b). Breaking continuous flash suppression: a new measure of unconscious processing during interocular suppression? *Front. Hum. Neurosci.* 5:167. doi: 10.3389/fnhum.2011.00167

Stein, T., Seymour, K., Hebart, M. N., and Sterzer, P. (2014). Rapid fear detection relies on high spatial frequencies. *Psychol. Sci.* 25, 566–574. doi: 10.1177/0956797613512509

Stein, T., Peelen, M. V., and Sterzer, P. (2012a). Eye gaze adaptation under interocular suppression. *J. Vis.* 12:1. doi: 10.1167/12.7.1

Stein, T., Sterzer, P., and Peelen, M. V. (2012b). Privileged detection of conspecifics: evidence from inversion effects during continuous flash suppresssion. *Cognition* 125, 64–79. doi: 10.1016/j.cognition.2012.06.005

Sterzer, P., Haynes, J. D., and Rees, G. (2008). Fine-scale activity patterns in high-level visual areas encode the category of invisible objects. *J. Vis.* 8, 1–12. doi: 10.1167/8.15.10

Sterzer, P., Hilgenfeldt, T., Freudenberg, P., Bermpohl, F., and Adli, M. (2011). Access of emotional information to visual awareness in patients with major depressive disorder. *Psychol. Med.* 41, 1615–1624. doi: 10.1017/S0033291710002540

Stewart, L. H., Ajina, S., Getov, S., Bahrami, B., Todorov, A., and Rees, G. (2012). Unconscious evaluation of faces on social dimensions. *J. Exp. Psychol. Gen.* 141, 715–727. doi: 10.1037/a0027950

Stoerig, P., and Cowey, A. (1997). Blindsight in man and monkey. *Brain* 120, 535–559. doi: 10.1093/brain/120.3.535

Stuit, S. M., Cass, J., Paffen, C. L. E., and Alais, D. (2009). Orientation-tuned suppression in binocular rivalry reveals general and specific components of rivalry suppression. *J. Vis.* 9, 17.1–17.15. doi: 10.1167/9.11.17

Sweeny, T. D., Grabowecky, M., and Suzuki, S. (2011). Awareness becomes necessary between adaptive pattern coding of open and closed curvatures. *Psychol. Sci.* 22, 943–950. doi: 10.1177/0956797611413292

Sylvers, P. D., Brennan, P. A., and Lilienfeld, S. O. (2011). Psychopathic traits and preattentive threat processing in children: a novel test of the fearlessness hypothesis. *Psychol. Sci.* 22, 1280–1287. doi: 10.1177/0956797611420730

Thompson, P., and Burr, D. (2009). Visual aftereffects. *Curr. Biol.* 19, R11–R14. doi: 10.1016/j.cub.2008.10.014

Troiani, V., and Schultz, R. T. (2013). Amygdala, pulvinar, and inferior parietal cortex contribute to early processing of faces without awareness. *Front. Hum. Neurosci.* 7:241. doi: 10.3389/fnhum.2013.00241

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Tsuchiya, N., Koch, C., Gilroy, L. A., and Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *J. Vis.* 6, 1068–1078. doi: 10.1167/6.10.6

Tsuchiya, N., Moradi, F., Felsen, C., Yamazaki, M., and Adolphs, R. (2009). Intact rapid detection of fearful faces in the absence of the amygdala. *Nat. Neurosci.* 12, 1224–1225. doi: 10.1038/nn.2380

van Boxtel, J. J. A., Tsuchiya, N., and Koch, C. (2010a). Consciousness and attention: on sufficiency and necessity. *Front. Psychol.* 1:217. doi: 10.3389/fpsyg.2010.00217

van Boxtel, J. J. A., Tsuchiya, N., and Koch, C. (2010b). Opposing effects of attention and consciousness on afterimages. *Proc. Natl. Acad. Sci. U.S.A.* 107, 8883–8888. doi: 10.1073/pnas.0913292107

Vizueta, N., Patrick, C. J., Jiang, Y., Thomas, K. M., and He, S. (2011). Dispositional fear, negative affectivity, and neuroimaging response to visually suppressed emotional faces. *Neuroimage* 59, 761–771. doi: 10.1016/j.neuroimage.2011.07.015

Vuilleumier, P., Armony, J. L., Driver, J., and Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nat. Neurosci.* 6, 624–631. doi: 10.1038/nn1057

Walker, P. (1978). Binocular rivalry: central or peripheral selective processes? *Psychol. Bull.* 85, 376–389. doi: 10.1037/0033-2909.85.2.376

Watanabe, K., Paik, Y., and Blake, R. (2004). Preserved gain control for luminance contrast during binocular rivalry suppression. *Vision Res.* 44, 3065–3071. doi: 10.1016/j.visres.2004.07.011

Watanabe, M., Cheng, K., Murayama, Y., Ueno, K., Asamizuya, T., Tanaka, K., et al. (2011). Attention but not awareness modulates the BOLD signal in the human V1 during binocular suppression. *Science* 334, 829–831. doi: 10.1126/science.1203161

Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., et al. (2004). Human amygdala responsivity to masked fearful eye whites. *Science* 306:2061. doi: 10.1126/science.1103617

Wheatstone, C. (1838). On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philos. Trans. R. Soc. Lond.* 128, 371–394. doi: 10.1098/rstl.1838.0019

Wilke, M., Logothetis, N. K., and Leopold, D. A. (2003). Generalized flash suppression of salient visual targets. *Neuron* 39, 1043–1052. doi: 10.1016/j.neuron.2003.08.003

Willenbockel, V., Lepore, F., Nguyen, D. K., Bouthillier, A., and Gosselin, F. (2012). Spatial frequency tuning during the conscious and non-conscious perception of emotional facial expressions- an intracranial ERP study. *Front. Psychol.* 3:237. doi: 10.3389/fpsyg.2012.
00237

Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Res.* 24, 471–478. doi: 10.1016/0042-6989(84)90044-0

Wolfe, J. M., Horowitz, T. S., Van Wert, M. J., Kenner, N. M., Place, S. S., and Kibbi, N. (2007). Low target prevalence is a stubborn source of errors in visual search tasks. *J. Exp. Psychol. Gen.* 136, 623–638. doi: 10.1037/0096-3445.136.4.623

Xu, S., Zhang, S., and Geng, H. (2011). Gaze-induced joint attention persists under high perceptual load and does not depend on awareness. *Vision Res.* 51, 2048–2056. doi: 10.1016/j.visres.2011.07.023

Yang, E., and Blake, R. (2012). Deconstructing continuous flash suppression. *J. Vis.* 12, 1–14. doi: 10.1167/12.3.8

Yang, E., Blake, R., and McDonald, J. E. (2010a). A new interocular suppression technique for measuring sensory eye dominance. *Investig. Ophthalmol. Vis. Sci.* 51, 588–593. doi: 10.1167/iovs.08-3076

Yang, E., Hong, S. W., and Blake, R. (2010b). Adaptation aftereffects to facial expressions suppressed from visual awareness. *J. Vis.* 10, 1–13. doi: 10.1167/10.12.24

Yang, E., McHugo, M., Dukic, M., Blake, R., and Zald, D. (2012). Advantage of fearful faces in breaking interocular suppression is preserved after amygdala lesions. *J. Vis.* 12:679. doi: 10.1167/12.9.679

Yang, E., Zald, D. H., and Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion* 7, 882–886. doi: 10.1037/1528-3542.7.4.882

Yang, Y., Rose, D., and Blake, R. (1992). On the variety of percepts associated with dichoptic viewing of dissimilar monocular stimuli. *Perception* 21, 47–62. doi: 10.1068/p210047

Yang, Y. H., and Yeh, S. L. (2010). Accessing the meaning of invisible words. *Conscious. Cogn.* 20, 223–233. doi: 10.1016/j.concog.2010.07.005

Yang, Z., Zhao, J., Jiang, Y., Li, C., Wang, J., Weng, X., et al. (2011). Altered negative unconscious processing in major depressive disorder: an exploratory neuropsychological study. *PLoS ONE* 6:e21881. doi: 10.1371/journal.pone.0021881

Yokoyama, T., Noguchi, Y., and Kita, S. (2013). Unconscious processing of direct gaze: evidence from an ERP study. *Neuropsychologia* 51, 1161–1168. doi: 10.1016/j.neuropsychologia.2013.04.002

Yu, K., and Blake, R. (1992). Do recognizable figures enjoy an advantage in binocular rivalry? *J. Exp. Psychol. Hum. Percept. Perform.* 18, 1158–1173. doi: 10.1037/0096-1523.18.4.1158

Yuval-Greenberg, S., and Heeger, D. J. (2013). Continuous flash suppression modulates cortical activity in early visual cortex. *J. Neurosci.* 33, 9635–9643. doi: 10.1523/JNEUROSCI.4612-12.2013

Zabelina, D. L., Guzman-Martinez, E., Ortega, L., Grabowecky, M., Suzuki, S., and Beeman, M. (2013). Suppressed semantic information accelerates analytic problem solving. *Psychon. Bull. Rev.* 20, 581–585. doi: 10.3758/s13423-012-0364-1

Zadbood, A., Lee, S. H., and Blake, R. (2011). Stimulus fractionation by interocular suppression. *Front. Hum. Neurosci.* 5:135. doi: 10.3389/fnhum.2011.00135

Zhou, W., Jiang, Y., He, S., and Chen, D. (2010). Olfaction modulates visual perception in binocular rivalry. *Curr. Biol.* 20, 1356–1358. doi: 10.1016/j.cub.2010.05.059

Zimba, L. D., and Blake, R. (1983). Binocular rivalry and semantic processing: out of sight, out of mind. *J. Exp. Psychol. Hum. Percept. Perform.* 9, 807–815. doi: 10.1037/0096-1523.9.5.807

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 17 March 2014; paper pending published: 21 May 2014; accepted: 23 June 2014; published online: 11 July 2014.

*Citation: Yang E, Brascamp J, Kang M-S and Blake R (2014) On the use of continuous flash suppression for the study of visual processing outside of awareness. Front. Psychol. **5**:724. doi: 10.3389/fpsyg.2014.00724*

This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

REVIEW ARTICLE
published: 23 May 2014
doi: 10.3389/fpsyg.2014.00460

Breaking continuous flash suppression: competing for consciousness on the pre-semantic battlefield

Surya Gayet*, Stefan Van der Stigchel and Chris L. E. Paffen

Experimental Psychology, Utrecht University, Utrecht, Netherlands

Edited by:
Nathan Faivre, California Institute of Technology, USA

Reviewed by:
Zhicheng Lin, University of Washington, USA
Wendy Jo Adams, University of Southampton, UK

****Correspondence:***
Surya Gayet, Experimental Psychology, Utrecht University, Heidelberglaan 1, Langeveld building, Room H0.56, Utrecht, Netherlands
e-mail: s.gayet@uu.nl

Traditionally, interocular suppression is believed to disrupt high-level (i.e., semantic or conceptual) processing of the suppressed visual input. The development of a new experimental paradigm, breaking continuous flash suppression (b-CFS), has caused a resurgence of studies demonstrating high-level processing of visual information in the absence of visual awareness. In this method the time it takes for interocularly suppressed stimuli to breach the threshold of visibility, is regarded as a measure of access to awareness. The aim of the current review is twofold. First, we provide an overview of the literature using this b-CFS method, while making a distinction between two types of studies: those in which suppression durations are compared between different stimulus classes (such as upright faces versus inverted faces), and those in which suppression durations are compared for stimuli that either match or mismatch concurrently available information (such as a colored target that either matches or mismatches a color retained in working memory). Second, we aim at dissociating high-level processing from low-level (i.e., crude visual) processing of the suppressed stimuli. For this purpose, we include a thorough review of the control conditions that are used in these experiments. Additionally, we provide recommendations for proper control conditions that we deem crucial for disentangling high-level from low-level effects. Based on this review, we argue that crude visual processing suffices for explaining differences in breakthrough times reported using b-CFS. As such, we conclude that there is as yet no reason to assume that interocularly suppressed stimuli receive full semantic analysis.

Keywords: continuous flash suppression, visual awareness, consciousness, binocular rivalry, interocular competition, interocular suppression

INTRODUCTION

INTEROCULAR COMPETITION

When different images are presented to both eyes, observers tend to perceive only one of these images, whereas the other one does not give rise to a conscious percept (e.g., binocular rivalry, Alais and Blake, 2005; flash suppression, Wolfe, 1984; continuous flash suppression, Tsuchiya and Koch, 2005). Under certain conditions the suppressed image has the potency to affect behavior, but this depends on the required level of processing (for a review see, Lin and He, 2009). For instance, the potency of low-level image properties, such as spatial frequency (Blake and Fox, 1974; Blake et al., 2006), motion direction (Wade and Wenderoth, 1978; O'Shea and Crassini, 1981; Blake et al., 1999), color (White et al., 1978), and orientation (Wade and Wenderoth, 1978) to elicit behavioral adaptation effects is relatively unaffected by interocular suppression. Conceptual or semantic processing, however, is traditionally believed to be abolished for interocularly suppressed stimuli (e.g., Zimba and Blake, 1983; Cave et al., 1998; Blake and Logothetis, 2002; Dehaene et al., 2006; Kang et al., 2011). In general, the extent to which neural activity reflects interocularly suppressed stimulation decreases gradually when climbing up the visual hierarchy (Blake and Logothetis, 2002). For instance, most cells in early visual areas (80% in V1/V2 and 60% in V4/V5) respond to stimulation of either eye irrespective of the dominant percept (Logothetis, 1998). Higher processing areas such as IT, FFA, and PPA, however, follow mostly (although not exclusively; Fang and He, 2005; Jiang and He, 2006; Sterzer et al., 2008) the dominant percept (Tong et al., 1998). Thus, interocularly suppressed stimuli are expected to be processed at the level of features and coarse feature configurations, which we will refer to as the lower or visual processing level, but not at a semantic or conceptual level (Blake and Logothetis, 2002), which we will refer to as higher level.

In contrast to this traditional view, studies using a novel paradigm called breaking continuous flash suppression (b-CFS; Jiang et al., 2007) seem to demonstrate that high-level processing of interocularly suppressed stimuli can occur prior to conscious experience. In the present article we aim to demonstrate that the seemingly high-level effects obtained in these b-CFS studies can be accounted for by coarse visual processing of the stimuli under continuous flash suppression (CFS). For this purpose, we provide a complete overview of all studies up to date (30) using b-CFS. Additionally, we suggest a number of improvements to the b-CFS method that help dissociate competition at relatively high levels of processing (i.e., at a conceptual or semantic level) from competition at lower levels of processing (i.e., at a featural level, where color, orientation, etc. are processed).

BREAKING CONTINUOUS FLASH SUPPRESSION

In the b-CFS paradigm, a high contrast dynamic pattern mask is presented to one eye, thereby effectively suppressing a stimulus of increasing intensity presented to the other eye. Eventually, the ocular dominance will reverse, such that the previously suppressed stimulus becomes visible. The time it takes for observers to detect the suppressed stimulus is assumed to reflect the moment in time at which the stimulus gains access to consciousness. Importantly, non-ocular factors can affect the moment at which interocularly suppressed stimuli become consciously observable (Blake, 2001; Paffen and Alais, 2011). In light of the b-CFS paradigm, we dissociate two factors that co-determine the timing of an ocular dominance reversal. First, some stimulus classes might inherently breach the threshold of visibility faster than other stimulus classes (e.g., upright versus inverted faces; Jiang et al., 2007). Second, suppression durations can systematically differ for stimuli that either match or mismatch consciously accessible information (e.g., prime-target congruency; Costello et al., 2009). In reviewing the b-CFS literature we propose to take into account these two distinct ways in which non-ocular factors impinge upon the selection for conscious access: manipulations of the content of the suppressed stimulus, and manipulations of the context within which the suppressed stimulus is presented. As both types of experiments have their own advantages and limitations in uncovering the nature of preconscious processes, they are discussed separately.

EFFECTS OF STIMULUS CONTEXT

PRIMING

The first part of this review comprises an overview of b-CFS studies in which the detection time of identical stimuli is compared between different experimental conditions. These studies show that the same visual input can result in different suppression durations depending on the (consciously accessible) context that is provided. One widely studied way to affect the context within which information is presented is priming. This method involves presenting a stimulus prior to the b-CFS task, which is either related or unrelated to the masked target stimulus. Costello et al. (2009) showed that written words (e.g., “fire”) break through suppression faster when they are preceded by a word that shares sub-word components (e.g., “tire”) than when they are preceded by a word that does not share sub-word components. Costello et al. (2009) also showed that words break through suppression faster when they are preceded by a semantically related word (e.g., “burn”) than when they are preceded by an unrelated word. Lupyan and Ward (2013) took this one step further by showing that this priming effect also occurs when prime and target are presented in different modalities; for instance, an image of a pumpkin broke through suppression faster after observers heard the word “pumpkin” than after hearing a word that did not match with the subsequent target. Yang and Yeh (2014) presented words under CFS, of which the onset was either accompanied by an audible white noise burst or not. Detection times were shortened by the concurrent presentation of noise bursts, but only when the audio and visual information originated from the same depth plane. Together, these priming studies reveal that visual input that matches previously perceived information breaks through suppression faster than visual input that mismatches this information. Importantly, the prime-target relation can be spatial, physical, or semantic in nature, and does not require presentation in the same modality.

THE CONTENT OF VISUAL WORKING MEMORY

Similarly to priming, the content of visual working memory is also known to affect visual processing, such that stimuli matching this content receive privileged processing compared to non-matching information (e.g., in search tasks, Olivers et al., 2006). One major difference between these two methods is that visual working memory involves the active, rather than passive maintenance (i.e., rehearsal) of visual features. In experiments that manipulate the content of visual working memory, participants are instructed to retain some feature of a visual stimulus for subsequent recollection. During the retention phase, participants perform a b-CFS task in which interocularly suppressed targets either match or mismatch the information that is concurrently retained in working memory. Recently, it has been shown that target stimuli under CFS are detected faster when they match rather than mismatch a color category (Gayet et al., 2013), an orientation (Liu et al., 2013) or a face (Pan et al., 2013) that is actively held in visual working memory. Crucially, detection times remain unaffected when the stimuli, otherwise used for the memory task, are passively viewed, as opposed to actively retained in working memory. In contrast with the priming studies discussed previously, Gayet et al. (2013) demonstrated that privileged detection of matching stimuli was only observed when the relevant stimulus dimension was retained; when participants retained the shape of a stimulus, targets that matched the color of that stimulus were not prioritized for conscious detection. Together, these working memory studies show that visual input that matches concurrently retained, task relevant information is accessible to consciousness faster than non-matching information.

SIMULTANEOUS CROSS MODAL PRIMING

Three recent studies used a methodological approach in which the manipulation of the context was longer lasting than that of priming studies, without involving the active retention of information as in the working memory studies. In these experiments, consciously accessible, non-visual information was concurrently presented with a b-CFS task. First, Zhou et al. (2010) demonstrated that images matching olfactory information (e.g., an image of a rose concurrently presented with the scent of a rose) break through suppression faster than images mismatching olfactory information (e.g., an image of a rose concurrently presented with the scent of butanol). Second, Alsius and Munhall (2013) showed that an interocularly suppressed talking face stimulus broke through suppression faster when an auditory sentence matched rather than mismatched the lip synchronization of the face. Finally, Salomon et al. (2013) showed an effect of proprioception on visual awareness. In their study, participants reported the orientation of an interocularly suppressed target, which was superimposed on a task-irrelevant image of a hand. This hand could either be congruent or incongruent with the participants' actual position. Targets broke through interocular suppression faster when the image of the hand matched the position of the real hand. The authors conclude that proprioception modulates the selection for conscious access of visual stimuli. Taken together, these studies show an advantage for detecting stimuli that match rather than mismatch consciously accessible information.

VISUAL VERSUS CONCEPTUAL ANALYSIS OF SUPPRESSED STIMULI

The major advantage of all b-CFS experiments described in Sections "Priming to Simultaneous Cross Modal Priming is that differences in suppression durations cannot be accounted for by differences in image characteristics between conditions. This follows from the fact that in all conditions the same stimuli are used as target stimuli under CFS. The differentiation between conditions stems purely from the relation between target stimuli and the consciously accessible context in which they are embedded. Arguably, this context biases the competition by boosting or diminishing the effective strength of the suppressed stimuli (for a similar interpretation for attention's effect on interocular suppression, see Paffen and Alais, 2011). The authors of the papers described above generally interpret their findings in terms of pre-activation of prime related information (either semantic or physical), which biases subsequent interocular competition (e.g., Lupyan and Ward, 2013). In this view, prime induced activity in areas further up the processing hierarchy (e.g., object selective areas) feeds back to the earlier visual cortex where the interocular competition is resolved (e.g., Blake, 1989; Tong, 2001). Note, however, that this interpretation cannot provide a satisfactory account for the semantic priming effect of Costello et al. (2009), which requires semantic analysis of the prime as well as the suppressed target. This issue is further discussed in Section "Assessing the Level of Processing."

The assumption that competition occurred at the level of simple stimulus features rather than at the semantic or conceptual level was explicitly tested by Lupyan and Ward (2013) in a second experiment. Here, participants were cued with either the word "square" or "circle," before performing a b-CFS task. By using a wide range of stimulus shapes ranging on a continuum from square to circle, they found that the similarity between the target stimulus and the cued shape was negatively correlated with the detection time of the target stimulus. The authors conclude from this finding that upon hearing (or reading) a word, a visual representation of its content is automatically activated. This active representation then facilitates subsequent detection of matching visual input. As such, the effects of semantic primes on suppression durations of subsequently presented targets are visual, rather than semantic in nature. The major advantage of this interpretation is that it allows for semantic priming, in the absence of semantic analysis of the suppressed stimulus.

Further support for this idea of feature pre-activation comes from the working memory experiments described above. When observers actively retain stimulus features, such as an orientation, these features can be decoded from activity in the early visual cortex (Harrison and Tong, 2009; Serences et al., 2009; Christophel et al., 2012). Thus, the abovementioned working memory studies allow for comparing between the situation in which prime-induced activity is retained and conditions in which prime-induced activity is discarded. The absence of an effect of the prime on suppression durations when the prime is perceived but not actively retained suggests that the prime-target congruency effects are indeed caused by pre-activation of prime induced features.

Together, the findings in this chapter show that providing a consciously accessible context prioritizes visual information that matches this context. As argued earlier, the consciously accessible context might activate a visual representation, which then interacts with the interocularly suppressed target. As such, even if the relation between the context and the suppressed target is semantic in nature, semantic analysis of the target is not *necessary* for detection times to be affected. One of the drawbacks of this type of b-CFS experiment is, however, that it does not allow for unequivocally excluding the possibility that the interocularly suppressed stimulus is processed up to a semantic level. In contrast, when comparing the potency of different stimulus classes in reaching visual awareness without providing a context, any difference in detection times between conditions (either featural or semantic in nature) reflects differences in the processing of the suppressed stimulus itself, rather than its interaction with a previously altered neural state. Studies using this approach will be discussed in the following paragraphs.

EFFECTS OF STIMULUS CONTENT

VISUAL CHARACTERISTICS

The second type of b-CFS experiments compares detection times between different stimulus categories. This comprises the comparison of stimulus categories that differ on the basis of relatively low-level visual properties that can be resolved in the early visual cortex, which will be discussed in this first section. For these stimulus properties, there is a tendency that more conspicuous stimuli are harder to suppress by CFS and, as such, break through suppression faster than less conspicuous stimuli. For instance, both higher contrast stimuli (Tsuchiya and Koch, 2005) and higher spatial frequency stimuli break through CFS more readily (Tsuchiya and Koch, 2005; Yang and Blake, 2012). Also, certain topological properties of interocularly suppressed stimuli elicit faster detection times than others. For instance, suppressed stimuli with a hole are detected faster than open stimuli made up of the same structural elements (Meng et al., 2012). When identical stimuli follow different motion patterns, this may result in different detection thresholds as well. For instance, coherently moving dot arrays break through suppression more often than random dot arrays that are presented for the same duration (Kaunitz et al., 2013). Climbing further up the visual hierarchy, images with strong grouping cues, such as Kanisza triangles are detected faster than non-Kanisza's made up of the same constituents (Wang et al., 2012). Together, these studies show that different stimuli yield different suppression durations, and that this effect might be linked to the saliency of the suppressed stimulus. This is in line with findings from binocular rivalry experiments, which demonstrate that the location at which a perceptual transition is initiated depends on the local saliency of the suppressed stimulus (Paffen et al., 2008; Stuit et al., 2010).

Differences in suppression durations between stimulus categories can be accounted for both by properties of the suppressed stimuli *per se*, and by interactions between properties of the stimuli and properties of the masks (for a discussion, see Stein et al., 2011a). We dissociate two types of interactions between the stimuli and the masks that can potentially affect suppression durations. First, increased differences between visual characteristics of the suppressed image and the CFS stimuli reduce the suppression strength. For instance, Yang and Blake (2012) showed that stimuli with oblique orientations broke through suppression faster than stimuli with cardinal orientations, when using traditional "Mondrians" as CFS stimulus (which contain only cardinal orientations). More specifically, greater similarity in spatial frequency content and orientation between the competing percepts led to stronger suppression in both b-CFS (Yang and Blake, 2012) and binocular rivalry (Stuit et al., 2011). Second, when the previously suppressed image (or a sub-part of it) breaks through suppression, detection is facilitated if the suppressed image and the masks are very different. As discerning a suppressed stimulus through a mask requires exceeding some threshold of certainty, stimuli with more "proof" of being a potential target have an advantage in breaking CFS (for similar interpretations, see Kaunitz et al., 2013 and Yang and Yeh, 2014). Such a bias could be underpinned by the phenomenon of piecemeal rivalry, which allows for perceiving local parts of the "suppressed" stimulus (Blake et al., 1992; O'Shea et al., 1997). Since the dominant percept is highly dynamic (i.e., the CFS masks), locally dominant stimulus parts from the non-dominant eye (in which the target is presented) are easily confused with the CFS masks, and thus disregarded. However, when piecemeal rivalry reveals stimulus parts that seem coherently related (e.g., they follow a particular pattern or movement direction), these stimulus parts may attract attention, as they are likely to be the target (e.g., collinear facilitation; Wilson et al., 2001). This may affect suppression durations, since attending to a stimulus in a specific eye enhances the competition strength of the entire ipsi-ocular stimulus (Ooi and He, 1999; Zhang et al., 2012).

Nonetheless, differences between aforementioned conditions do not necessitate non-conscious semantic or conceptual processing, but are based on the differentiation of stimulus properties that are generally assumed to survive interocular suppression (for reviews, see Blake and Logothetis, 2002; Lin and He, 2009; Faivre et al., 2014; Sterzer et al., 2014). In the next sections, a number of studies will be discussed in which suppression durations are affected on the basis of higher level stimulus properties (i.e., at a semantic or conceptual level). Please note that the "familiarity" and "ecological relevance" distinction, as provided below, aims at categorizing these studies based on topical similarities, rather than describing the mechanisms that drive their results.

FAMILIARITY

Differences in detection times between stimulus categories can also arise on the basis of more high-level distinctions, such as stimulus familiarity. For instance, images of human bodies or body parts are detected faster when presented upright as compared to inverted (Stein et al., 2012). As the authors demonstrate that this latter effect was abolished when the images were distorted, the authors argue that the difference in detection times is accounted for by the greater familiarity of upright human bodies. Along the same lines, upright faces are detected faster than inverted faces (Jiang et al., 2007; Zhou et al., 2010; Stein et al., 2011a,b; Gray et al., 2013). Two of these studies (Stein et al., 2011b; Gray et al., 2013) also included a polarity inversion condition, demonstrating that detection times were fastest for normal faces (upright and normal polarity) and slowest for the most unusual face presentation condition (spatial inversion and inversed polarity), although the inversion effect was only marginally significant in the inversed polarity condition of Stein et al. (2011b). The finding that face inversion effects are dependent on (or additive to) manipulations of the contrast polarity, supports the idea that it is indeed familiarity that drives the priority for detecting upright faces. Importantly, however, Stein et al. (2011b) replicated these findings with configurations of three blobs representing two eyes and a mouth. This demonstrates that the privilege for detecting upright faces can be resolved by very crude visual processing.

Gobbini et al. (2013b) took the manipulation of stimulus familiarity even further by showing that interocularly suppressed familiar faces are detected faster than faces of strangers. A more subtle finding comes from a study showing that faces from the own racial in-group break through suppression faster than faces from the racial out-group (Stein, 2012). That same study showed that faces of the same age group as that of the observer break through suppression faster than faces of another age group. Importantly, the differences in suppression durations between image conditions were computed relative to that of inverted faces, such that they could not be attributed to differences in low-level image properties (see Control 1: Disrupting the Extraction of Meaning). Rather, the authors suggest that this effect is accounted for by the observer's greater visual expertise with stimuli of the own-race and own-age stimulus classes.

This facilitatory effect for detecting visual input of higher familiarity is also found for stimuli that are more recently acquired in evolutionary time, such as written language. Indeed, words in a familiar alphabet are detected faster than words in an alphabet that is unfamiliar to the observer (Jiang et al., 2007). Similarly, Chinese characters are detected faster by Chinese readers compared to the same characters that have been inversed or scrambled (Yang and Yeh, 2011, 2014). Taken together, these studies show that visual input with higher stimulus familiarity is more readily detected than less familiar input. Arguably, extended experience with certain types of stimuli might facilitate subsequent detection. If so, the factor of familiarity might be the long term equivalent of the stimulus feature pre-activation as described in Section "Effects of Stimulus Context."

ECOLOGICAL RELEVANCE

A number of studies demonstrate differences in detection times for stimuli that differ on the basis of ecological relevance. For instance, observers show an advantage for detecting faces turned toward the observer compared to faces turned slightly away from the observer (Gobbini et al., 2013a). This difference was found to be independent of the gaze direction of the face. Similarly, faces with direct gaze break through interocular suppression faster than faces with averted gaze. This was found both for schematic faces (Chen and Yeh, 2012) and for face photographs (Stein et al., 2011c). This advantage for detecting faces with direct gaze could not be explained by (lower-level) effects of eye symmetry, as Stein et al. (2011c) included images of both frontal faces and laterally averted faces, such that gaze direction should be inferred by the particular combination of both face orientation and pupil position. However, the advantage in detecting stimuli with direct gaze over averted gaze persisted for inverted faces (Stein et al., 2011c; Chen and Yeh, 2012). Gaze direction in (visible) faces is more difficultly inferred from inverted faces compared to upright faces (e.g., Vecera and Johnson, 1995). Thus, the effect of gaze direction on detection times should be less prominent in the inverted condition than in the upright condition. The absence of this interaction between gaze direction and face inversion therefore hints toward the interpretation that crude configural differences between gaze conditions might play a causal role in eliciting these differences in detection times. For instance, Chen and Yeh (2012) propose that the specific conjunction of face curvature and pupil location is sufficient in eliciting shorter suppression durations. In line with this idea, they demonstrated in an additional experiment that the mere schematic depiction of eyes was sufficient in explaining the observed difference in detection times of full (schematic) faces.

Another ecologically potentially relevant distinction between stimulus categories is that of emotional versus non-emotional stimuli. For instance, fearful faces break through suppression faster than neutral faces (Yang et al., 2007; Gray et al., 2013; Stein et al., 2014) or happy faces (Yang et al., 2007; Tsuchiya et al., 2009; Gray et al., 2013), while happy (Yang et al., 2007) and angry faces (Gray et al., 2013) break through suppression *slower* than neutral faces. Interestingly, both types of emotional expressions break through suppression *faster* than neutral faces when schematic face images are used instead of face photographs (Stein and Sterzer, 2012). This contradiction suggests that it is not the analysis of the emotional valence *per se*, but rather the visual properties of the image that affected suppression durations in these studies. In line with this lower level account, the findings of Gray et al. (2013) persisted for inverted faces and for faces with inversed polarity, while the findings of Yang et al. (2007) persisted for inverted faces and for eyes-only images. Similarly, the findings of Stein and Sterzer (2012) were fully accounted for by the relative orientation of the mouth curvature and the face contour. Finally, the findings of Stein et al. (2014) depended solely on high spatial frequency information. Since subcortical (i.e., amygdala) processing of fearful faces relies predominantly on low spatial frequency information (e.g., LeDoux, 1998), this finding suggests that non-conscious processing of fearful faces is dependent on cortical processing. Patient SM, who has complete bilateral amygdala lesions and is unable to consciously discriminate between fearful and happy faces, showed the same advantages for detecting CFS-suppressed fearful faces over happy faces as controls did (Tsuchiya et al., 2009). As such, non-conscious discrimination between emotional faces seems to rely more on (cortical) extraction of characteristic visual features, than on the (subcortical) analysis of the emotional valence *per se*. Taken together, these studies show a tendency for ecologically relevant stimuli to break through interocular suppression faster than less ecologically relevant stimuli. However, most of these effects have been shown to rely on stimulus properties, or stimulus configurations, that can be dissociated on the basis of relatively crude visual processing. In sum, semantic, conceptual or emotional analysis of interocularly suppressed stimuli is not a *necessary* condition to account for the observed differences in detection times. Rather, the extraction of purely visual information seems to sufficient to explain most of the findings discussed so far.

CLIMBING TOWARD THE SEMANTIC AND CONCEPTUAL LEVEL

As with the privilege for detecting familiar stimuli, the privilege for detecting emotional stimuli was not restricted to evolutionarily old visual input, such as faces, but was also demonstrated for words (Yang and Yeh, 2011). Interestingly, the results of this study revealed that both (Chinese) words that *describe* a negative emotion (e.g., "anger" or "fear") and words that *induce* a negative emotion (e.g., "murder" or "abuse") were detected *later* than neutral words. Taking this idea even further, Sklar et al. (2012) compared suppression durations of emotionally negative expressions to suppression durations of neutral expressions. Importantly, the words that formed these expressions had no intrinsic emotional valence (e.g., "eternal" and "rest"; "eternal rest"). Nonetheless, the expressions with a negative emotional valence broke through suppression faster than neutral expressions. Interestingly, these results are at odds with that of Yang and Yeh (2011). Still, both studies demonstrate effects that require semantic processing of the words before interocular competition is resolved.

Sklar et al. (2012) also demonstrated that combinations of (Hebrew) words that yield incoherent expressions (e.g., "she ironed coffee") broke through suppression faster than coherent expressions (e.g., "she drank coffee"). Again, it is the semantic combination of words that determines whether an expression is coherent or incoherent, rather than the individual words themselves. This finding demonstrates that the meaning of words is indeed extracted and integrated non-consciously. Along the same lines, Mudrik et al. (2011) showed that scenes containing incongruent objects (e.g., Michael Jordan holding a watermelon) broke through suppression faster than the same scenes containing congruent objects (e.g., Michael Jordan holding a basketball). The authors stress that dissociating a coherent from an incoherent image requires the integration of an object in its semantic context; a process originally thought to require consciousness (e.g., Edelman and Tononi, 2000). In contrast with the familiarity effects discussed in Section "Familiarity," the stimuli used in these last two experiments seem too complex for the differences in suppression durations to be accounted for by differences in visual experience between stimulus conditions. As such, these results imply full blown semantic analysis of interocularly suppressed stimuli.

DISCUSSION

ASSESSING THE LEVEL OF PROCESSING

Most findings in Section "Priming" up to Section "Ecological Relevance" can be explained by preconscious analysis of suppressed stimuli at relatively early stages of visual processing. Whether they are caused by pre-activation of primed features, by the saliency of a stimulus, or by the long time strengthening of visual representations of relevant feature configurations, these findings do not seem to require semantic or conceptual processing. In contrast, the findings discussed in the last section (see Climbing Towards the Semantic and Conceptual Level) as well as the semantic priming effect of Costello et al. (2009) seem to defy the model of early competition in interocular suppression and point to high-level analysis of the suppressed stimuli. There are, however, two reasons to plead for caution in interpreting the studies that demonstrate these high-level effects (e.g., language and scene comprehension). First, some of the results described above seem contradictory, such as the results of Sklar et al. (2012) in which negative emotional expressions yielded shorter suppression durations compared to the results of Yang and Yeh (2011) in which negative emotional words yielded longer suppression durations. In a broader sense, the overall pattern of findings of these high-level effects (see Climbing Towards the Semantic and Conceptual Level) seems inconsistent with the pattern of findings from lower level effects (Sections Priming – Ecological Relevance). On the one hand, words and images break through suppression faster when they have a higher prevalence in the observers' visual world (i.e., when they are of higher familiarity). On the other hand, however, word combinations and complex scenes break through suppression faster when they are incongruent or novel, and thus are of lower familiarity. While it is conceivable that scene complexity influences the magnitude of the effect of familiarity on suppression durations, it is unexpected that scene complexity causes a reversal in the direction of the effect of familiarity on suppression durations.

Second, to demonstrate that differences in suppression durations are caused by competition at a high processing level (i.e., semantic or conceptual), it is important to implement a comparison with a condition that disrupts high-level processing, such as inversion (e.g., as used in the Sterzer lab), polarity inversion or scrambling. If the difference in suppression durations observed under normal presentation conditions is also apparent in these conditions, it is likely that the effect is caused by differences in lower level visual properties between the stimulus classes (see Control 1: Disrupting the Extraction of Meaning). Four out of five studies that do include this type of control conditions to dissociate between competition at higher processing levels from competition at lower (visual) processing levels, demonstrated that the effect could indeed be attributed to competition at lower levels of the processing hierarchy (Stein et al., 2011b; Stein and Sterzer, 2012; Chen and Yeh, 2012; Gray et al., 2013). Consequently, these studies do not attribute their findings to high level processing under continuous flash suppression. Importantly, three out of four b-CFS experiments that led the authors to conclude from their data that the observed difference in suppression durations was caused by semantic or conceptual analysis of the stimuli under CFS, however, did not include such a control condition (i.e., Costello et al., 2009; Mudrik et al., 2011; Sklar et al., 2012). Thus far, the only study that convincingly demonstrates high-level competition in a b-CFS experiment, is that of Yang and Yeh (2011). In this study, the authors included an inversion condition, a scrambled condition as well as a monocular condition. This revealed that the shorter suppression durations for neutral Chinese words compared to emotional Chinese words was only apparent in the upright unscrambled dichoptic condition.

In sum, more and more studies (discussed in Climbing Towards The Semantic and Conceptual Level) aim at demonstrating that semantic and conceptual information might be integrated non-consciously. However, this is hard to reconcile with studies showing that semantic priming effects are abolished under interocular suppression (e.g., Zimba and Blake, 1983; Cave et al., 1998; Kang et al., 2011; for reviews, see Lin and He, 2009; Faivre et al., 2014; Sterzer et al., 2014). In some studies interocular suppression is even used as a tool to disrupt semantic processing (e.g., Lupyan and Ward, 2013). These high-level effects are also hard to reconcile with the idea that interocular competition is resolved in early visual areas such as LGN (Haynes et al., 2005) and V1 (Polonsky et al., 2000). Although some interocularly suppressed information is known to transpire into higher visual areas (e.g., Fang and He, 2005; Jiang and He, 2006; Sterzer et al., 2008), succeeding levels in the processing hierarchy reveal less and less brain activity that reflects interocularly suppressed stimulation (Blake and Logothetis, 2002). Moreover, CFS is known to result in greater suppression depths than more traditional methods of interocular suppression, such as flash suppression and binocular rivalry (Tsuchiya et al., 2006). Consequently, when b-CFS is used to compare different classes of stimuli in their potency to breach the threshold of awareness, it is of utmost importance to test whether reaction times indeed reflect differences in high-level rather than low-level information in the stimuli. Additionally, irrespective of the processing level at which the competition takes place, it is crucial to assert whether reaction times indeed reflect differences in the timing at which a stimulus was available to consciousness, rather than processes arising after the stimulus became available to consciousness. These post-perceptual effects pose a threat to b-CFS experiments in which the stimulus content is manipulated as well as to experiments in which the stimulus context is manipulated. We propose that at least the following three control conditions should be included in b-CFS experiments to control for these potential pitfalls.

CONTROL 1: DISRUPTING THE EXTRACTION OF MEANING

To assess whether differences between conditions rely on high-level information (i.e., at a semantic or conceptual level), one or more conditions should be included that are known to disrupt the extraction of high-level image properties, while keeping low-level (i.e., visual) image properties relatively unaffected. This can be achieved by such manipulations as inverting the image or inverting the image polarity (e.g., Jiang et al., 2007; Zhou et al., 2010; Stein et al., 2011b; Chen and Yeh, 2012; Gray et al., 2013). These manipulations constrain the extraction of meaning from an image (Rock, 1974; Shore and Klein, 2000), such that high-level driven effects should at least diminish under these circumstances. As such, if some image class breaks through suppression faster than another stimulus class because of high-level (i.e., semantic or conceptual) differences, the differences in detection times between these two stimulus classes should not be observed (or at least diminish) when the images are presented upside down. Conversely, if the difference in detection times between two stimulus classes does persist with inverted presentation, this suggests that there are systematic low-level visual differences between the two image classes, as these should remain unaffected by inverted presentation. In that case, the differences in low-level visual properties are the probable cause of the difference in detection times between the two stimulus classes. For this reason, rather than looking at absolute detection times for each stimulus category, it is more informative to look at the inversion effect, which is described as the difference in detection times between upright and inverted stimuli of the same stimulus category. This difference can then be divided by the detection time of inverted stimuli (as in Stein, 2012) such as to remove the between subject variability in detection times. Consequently, to assess whether a difference between image classes relies on high-level stimulus processing, it is important to demonstrate that the inversion effects (rather than the detection times *per se*) differ between stimulus classes.

CONTROL 2: STIMULUS REPORTABILITY

Next, it is important to verify whether differences in reaction times indeed reflect differences in visual awareness. An alternative view is that differences in reaction times are driven by non-conscious processes, such that stimulus information is accessible only to the extent that it affects forced choice localization, while not being accessible to subjective report. Arguably, a stimulus fails to reach visual awareness, if it is accessible to one output system, but not to the other (Baars, 1993; Kanwisher, 2001). Thus, in order to conclude that some manipulation in a b-CFS experiment affects visual awareness, visual awareness should be measured directly. Visual awareness of a stimulus is assumed to be a prerequisite for stimulus reportability (Dehaene et al., 2006). As such, it can be operationalized as the ability to subjectively report ones percept (Dennett, 1993; Weiskrantz, 1997; Dehaene and Naccache, 2001). For the present purpose, a direct way to test whether one stimulus was accessible to consciousness and the other was not, is to compare participants' ability to report the identity of two concurrent stimuli at a particular point in time. This objective measure of stimulus reportability can be implemented by presenting two stimuli of different conditions simultaneously (e.g., one at either side of fixation). After participants perform a speeded detection of the location at which (e.g., left or right of fixation) they first see a stimulus appear, they should report either the identity of the percept on the reported location, or of that on the non-reported location. If no post-detection strategic bias is involved, participants should be significantly worse at reporting the identity of the stimulus on the non-reported location as compared to that of the reported location. Conversely, if participants are equally proficient at reporting the identity of either stimulus, one may not conclude that there was a difference in conscious access between stimulus conditions.

CONTROL 3: POST DETECTION EFFECTS

Finally, it is important to assess whether differences in detection times indeed reflect differences in interocular suppression durations, rather than processing differences arising after conscious detection of the stimulus (e.g., a difference in response criterion). To account for these "late" effects it is imperative to add a monocular (or binocular) control condition, in which the "suppressed" stimulus and the CFS are presented to the same eye(s). Specifically, we advocate the use of two different monocular control conditions (as in, Costello et al., 2009; and Gayet et al., 2013). First, a monocular control condition is needed in which the presentation times are identical to that of the interocular condition, such as to keep the stimulus chronology constant (i.e., a physically similar control). The disadvantage of this condition is, however, that reaction times in this condition are much faster than in the interocular condition. Consequently, any differences in reaction times between conditions are reduced in magnitude as well, as a result of which the experimental power can be diminished (although the variance is reduced as well). Thus, it is imperative to implement a second monocular condition such, that the reaction time distributions (means and SD's) match that of the interocular condition (for further discussion on this issue, see Stein et al., 2011a). This can be achieved by (1) lengthening the ramp of the "suppressed" stimulus, such as to mimic the longer suppression durations of trials with dichoptic presentation, and, (2) by jittering the target onset, such as to add uncertainty as to when the target will appear (i.e., a perceptually similar control). Ideally, interocular trials and monocular control trials are randomly intermixed within blocks. This has the main advantage of making the perceptual difference between dichoptic and monocular (or binocular) presentation conditions less conspicuous, due to the whimsical nature of dichoptically presented trials.

Together, these three methods provide empirical tests for (1) whether differences between stimulus conditions actually rely on high-level information, (2) whether differences in reaction times indeed reflect differences in explicit visual awareness, and (3) whether reaction times were affected by processing differences emerging after conscious detection, such as changes in response criterion.

INTERPRETING THE RESULTS OF b-CFS STUDIES

As mentioned in the introduction, the rationale underlying b-CFS experiments is that differences in suppression durations between conditions reflect different processing of stimuli prior to conscious access. An often disregarded alternative, however, is that differences between conditions may affect visual processing *during* the transitory period in which the interocularly suppressed stimuli gradually gain access to consciousness. In support of this latter idea, CFS allows for periods of partial awareness, in which some, but not all, features of a stimulus are suppressed (Zadbood et al., 2011; Yang and Blake, 2012). Crucially, Mudrik et al. (2013) demonstrated that "non-conscious" processing of faces was restricted to periods of partial awareness. This finding has two consequences for b-CFS studies: First, it indicates that detection tasks are better suited than discrimination tasks to ascertain that differences in detection times between conditions are initiated prior to a switch in ocular dominance. For instance, if the crucial manipulation involves one feature of some stimulus (e.g., color) and participants are required to report another feature of that stimulus (e.g., orientation) for the b-CFS task, it is conceivable that the color of that same stimulus was accessible to consciousness prior to its orientation. As a result, the possibility cannot be excluded that the process driving the differences in detection times between color conditions arose after the interocular competition (of that particular feature) was resolved, thereby reflecting a conscious rather than non-conscious process. Second, and more importantly, if the main goal of the experimenter is to uncover the nature of non-conscious processing, the concurrent usage of multiple suppression techniques is advisable, with an emphasis on the more traditional methods that have been ostensibly validated (Stein and Sterzer, 2014) and are less susceptible to partial awareness (Mudrik et al., 2013). As suggested above, b-CFS possibly relies on processing differences during the transitory period, in which previously suppressed stimuli gain gradual access to consciousness. As such, it is hard to ascertain whether differences in stimulus processing during a transition of ocular dominance can generalize to differences in stimulus processing in the complete absence of consciousness. Despite being not as well suited as a tool to uncover non-conscious processing *per se*, b-CFS experiments are nonetheless very informative as a measure of access to awareness (Stein and Sterzer, 2014). Consequently, the results of b-CFS experiments should be interpreted as such.

With the above mentioned additions to the b-CFS paradigm, we hope to provide the means to effectively dissociate situations in which competition for conscious access occurs on high-level battle grounds and thus requires conceptual or semantic processing, from situations in which the competition occurs on lower level battle grounds, such that crude visual processing of the suppressed stimuli suffices. In light of the abovementioned limitations, it should be emphasized that whether or not high-level stimulus properties exert influence on conscious access within the b-CFS paradigm does not necessarily imply that the same restrictions apply to non-conscious processing under CFS, let alone to interocular suppression in general. Thus far, however, the idea that interocularly suppressed stimuli are not analyzed up to semantic or conceptual processing levels has been mainly challenged by b-CFS experiments. The present review included 30 studies that use this experimental paradigm, of which 8 aimed to explore whether suppression durations could be affected by competition at a semantic or conceptual processing stage. Four of these studies demonstrate that these effects could be accounted for by differences in low-level visual properties, three of these studies did not include conditions that controls for differences in low-level visual properties, and as a result, only one study demonstrates high-level effects in a b-CFS task. As such, we conclude that interocular competition at a visual level is a sufficient explanation for most b-CFS studies that properly control for low-level visual differences (i.e., that include an inversion condition). As such, we should be reluctant to revise the traditional idea that semantic or conceptual analysis is abolished under interocular suppression.

ACKNOWLEDGMENTS

This research was funded by Grant 404-10-306 from the Netherlands Organization for Scientific Research to Stefan Van der Stigchel and Chris L. E. Paffen.

REFERENCES

Alais, D., and Blake, R. (2005). *Binocular Rivalry and Perceptual Ambiguity.* Boston, MA MIT Press.

Alsius, A., and Munhall, K. G. (2013). Detection of audiovisual speech correspondences without visual awareness. *Psychol. Sci.* 24, 423–431. doi: 10.1177/0956797612457378

Baars, B. J. (1993). *A Cognitive Theory of Consciousness.* Cambridge: Cambridge University Press.

Blake, R. (1989). A neural theory of binocular rivalry. *Psychol. Rev.* 96, 145–167. doi: 10.1037/0033-295X.96.1.145

Blake, R. (2001). A primer on binocular rivalry, including current controversies. *Brain Mind* 2, 5–38. doi: 10.1023/A:1017925416289

Blake, R., Ahlström, U., and Alais, D. (1999). Perceptual priming by invisible motion. *Psychol. Sci.* 10, 145–150. doi: 10.1111/1467-9280.00122

Blake, R., and Fox, R. (1974). Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature* 249, 488–490. doi: 10.1038/249488a0

Blake, R., and Logothetis, N. K. (2002). Visual competition. *Nat. Rev. Neurosci.* 3, 13–21. doi:10.1038/nrn701

Blake, R., O'Shea, R. P., and Mueller, T. J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. *Vis. Neurosci.* 8, 469–478. doi: 10.1017/S0952523800004971

Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., and Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 4783–4788. doi: 10.1073/pnas.0509634103

Cave, C. B., Blake, R., and McNamara, T. P. (1998). Binocular rivalry disrupts visual priming. *Psychol. Sci.* 9, 299–302. doi: 10.1111/1467-9280.00059

Chen, Y. C., and Yeh, S. L. (2012). Look into my eyes and I will see you: unconscious processing of human gaze. *Conscious. Cogn.* 21, 1703–1710. doi: 10.1016/j.concog.2012.10.001

Christophel, T. B., Hebart, M. N., and Haynes, J.-D. (2012). Decoding the contents of visual short-term memory from human visual and parietal cortex. *J. Neurosci.* 32, 12983–12989. doi: 10.1523/JNEUROSCI.0184-12.2012

Costello, P., Jiang, Y., Baartman, B., McGlennen, K., and He, S. (2009). Semantic and subword priming during binocular suppression. *Conscious. Cogn.* 18, 375–382. doi: 10.1016/j.concog.2009.02.003

Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., and Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn. Sci.* 10, 204–211. doi: 10.1016/j.tics.2006.03.007

Dehaene, S., and Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition* 79, 1–37. doi: 10.1016/S0010-0277(00)00123-2

Dennett, D. C. (1993). *Consciousness Explained.* London: Penguin.

Edelman, G. M., and Tononi, G. (2000). *A Universe of Consciousness: How Matter becomes Imagination.* New York: Basic books.

Faivre, N., Berthet, V., and Kouider, S. (2014). Sustained invisibility through crowding and continuous flash suppression: a comparative review. *Front. Psychol.* 5:475. doi: 10.3389/fpsyg.2014.00475

Fang, F., and He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nat. Neurosci.* 8, 1380–1385. doi: 10.1038/nn1537

Gayet, S., Paffen, C. L. E., and Van der Stigchel, S. (2013). Information matching the content of visual working memory is prioritized for conscious access. *Psychol. Sci.* 24, 2472–2480. doi: 10.1177/0956797613495882

Gobbini, M. I., Gors, J. D., Halchenko, Y. O., Hughes, H. C., and Cipolli, C. (2013a). Processing of invisible social cues. *Conscious. Cogn.* 22, 765–770. doi: 10.1016/j.concog.2013.05.002

Gobbini, M. I., Gors, J. D., Halchenko, Y. O., Rogers, C., Guntupalli, J. S., Hughes, H., et al. (2013b). Prioritized detection of personally familiar faces. *PLoS ONE* 8:e66620. doi: 10.1371/journal.pone.0066620

Gray, K. L., Adams, W. J., Hedger, N., Newton, K. E., and Garner, M. (2013). Faces and awareness: low-level, not emotional factors determine perceptual dominance. *Emotion* 13, 537–544. doi: 10.1037/a0031403

Harrison, S. A., and Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature* 458, 632–635. doi: 10.1038/nature07832

Haynes, J.-D., Deichmann, R., and Rees, G. (2005). Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature* 438, 496–499. doi: 10.1038/nature04169

Jiang, Y., Costello, P., and He, S. (2007). Processing of invisible stimuli: advantage of upright face and recognizable words in overcoming interocular suppression. *Psychol. Sci.* 18, 349–355. doi: 10.1111/j.1467-9280.2007.01902.x

Jiang, Y., and He, S. (2006). Cortical responses to invisible faces: dissociating subsystems for facial-information processing. *Curr. Biol.* 16, 2023–2029. doi: 10.1016/j.cub.2006.08.084

Kang, M. S., Blake, R., and Woodman, G. F. (2011). Semantic analysis does not occur in the absence of awareness induced by interocular suppression. *J. Neurosci.* 31, 13535–13545. doi: 10.1523/JNEUROSCI.1691-11.2011

Kanwisher, N. (2001). Neural events and perceptual awareness. *Cognition* 79, 89–113. doi: 10.1016/S0010-0277(00)00125-6

Kaunitz, L., Fracasso, A., Lingnau, A., and Melcher, D. (2013). Non-conscious processing of motion coherence can boost conscious access. *PLoS ONE* 8:e60787. doi: 10.1371/journal.pone.0060787

LeDoux, J. (1998). *The Emotional Brain: The Mysterious Underpinnings of Emotional Life.* New York: Simon and Schuster.

Lin, Z., and He, S. (2009). Seeing the invisible: the scope and limits of unconscious processing in binocular rivalry. *Prog. Neurobiol.* 87, 195–211. doi: 10.1016/j.pneurobio.2008.09.002

Liu, D., Wang, L., and Jiang, Y. (2013). Working memory modulates unconscious visual processing. *J. Vis.* 13, 802. doi: 10.1167/13.9.802

Logothetis, N. K. (1998). Single units and conscious vision. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 353, 1801–1818. doi: 10.1098/rstb.1998.0333

Lupyan, G., and Ward, E. J. (2013). Language can boost otherwise unseen objects into visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* 110, 14196–14201. doi: 10.1073/pnas.1303312110

Meng, Q., Cui, D., Zhou, K., Chen, L., and Ma, Y. (2012). Advantage of hole stimulus in rivalry competition. *PLoS ONE* 7:e33053. doi: 10.1371/journal.pone.0033053

Mudrik, L., Breska, A., Lamy, D., and Deouell, L. Y. (2011). Integration without awareness expanding the limits of unconscious processing. *Psychol. Sci.* 22, 764–770. doi: 10.1177/0956797611408736

Mudrik, L., Gelbard-Sagiv, H., Faivre, N., and Koch, C. (2013). Knowing where without knowing what: partial awareness and high-level processing in continuous flash suppression. *J. Vis.* 13, 1103. doi: 10.1167/13.9.1103

Olivers, C. L. N., Meijer, F., and Theeuwes, J. (2006). Feature-based memory-driven attentional capture: visual working memory content affects visual attention. *J. Exp. Psychol. Hum. Percept. Perform.* 32, 1243–1265. doi: 10.1037/0096-1523.32.5.1243

Ooi, T. L., and He, Z. J. (1999). Binocular rivalry and visual awareness: the role of attention. *Perception* 28, 551–574. doi: 10.1068/p2923

O'Shea, R. P., and Crassini, B. (1981). The sensitivity of binocular rivalry suppression to changes in orientation assessed by reaction-time and forced-choice techniques. *Perception* 10, 283–293. doi: 10.1068/p100283

O'Shea, R. P., Sims, A. J., and Govan, D. G. (1997). The effect of spatial frequency and field size on the spread of exclusive visibility in binocular rivalry. *Vision Res.* 37, 175–183. doi: 10.1016/S0042-6989(96)00113-7

Paffen, C. L., and Alais, D. (2011). Attentional modulation of binocular rivalry. *Front. Hum. Neurosci.* 5:105. doi: 10.3389/fnhum.2011.00105

Paffen, C. L., Naber, M., and Verstraten, F. A. (2008). The spatial origin of a perceptual transition in binocular rivalry. *PLoS ONE* 3:e2311. doi: 10.1371/journal.pone.0002311

Pan, Y., Lin, B., Zhao, Y., and Soto, D. (2013). Working memory biasing of visual perception without awareness. *Atten. Percept. Psychophys.* doi: 10.3758/s13414-013-0566-2 [Epub ahead of print].

Polonsky, A., Blake, R., Braun, J., and Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nat. Neurosci.* 3, 1153–1159. doi: 10.1038/80676

Rock, I. (1974). The perception of disoriented figures. *Sci. Am.* 230, 78–85. doi: 10.1038/scientificamerican0174-78

Salomon, R., Lim, M., Herbelin, B., Hesselmann, G., and Blanke, O. (2013). Posing for awareness: proprioception modulates access to visual consciousness in a continuous flash suppression task. *J. Vis.* 13, 2. doi: 10.1167/13.7.2

Serences, J. T., Ester, E. F., Vogel, E. K., and Awh, E. (2009). Stimulus-specific delay activity in human primary visual cortex. *Psychol. Sci.* 20, 207–214. doi: 10.1111/j.1467-9280.2009.02276.x

Shore, D. I., and Klein, R. M. (2000). The effects of scene inversion on change blindness. *J. Gen. Psychol.* 127, 27–43. doi: 10.1080/00221300009598569

Sklar, A. Y., Levy, N., Goldstein, A., Mandel, R., Maril, A., and Hassin, R. R. (2012). Reading and doing arithmetic nonconsciously. *Proc. Natl. Acad. Sci. U.S.A.* 109, 19614–19619. doi: 10.1073/pnas.1211645109

Stein, T. (2012). *Visual Processing of Social Information During Interocular Suppression.* Doctoral dissertation. Humboldt University, Berlin. Available at: http://edoc.hu-berlin.de. doi: d-nb.info/1025112334

Stein, T., Hebart, M. N., and Sterzer, P. (2011a). Breaking continuous flash suppression: a new measure of unconscious processing during interocular suppression? *Front. Hum. Neurosci.* 5:167. doi: 10.3389/fnhum.2011.00167

Stein, T., Peelen, M. V., and Sterzer, P. (2011b). Adults' awareness of faces follows newborns' looking preferences. *PLoS ONE* 6:e29361. doi: 10.1371/journal.pone.0029361

Stein, T., Senju, A., Peelen, M. V., and Sterzer, P. (2011c). Eye contact facilitates awareness of faces during interocular suppression. *Cognition* 119, 307–311. doi: 10.1016/j.cognition.2011.01.008

Stein, T., Seymour, K., Hebart, M. N., and Sterzer, P. (2014). Rapid fear detection relies on high spatial frequencies. *Psychol. Sci.* 566–574. doi: 10.1177/0956797613512509

Stein, T., and Sterzer, P. (2012). Not just another face in the crowd: detecting emotional schematic faces during continuous flash suppression. *Emotion* 12, 988–996. doi: 10.1037/a0026944

Stein, T., and Sterzer, P. (2014). Unconscious processing under interocular suppression: getting the right measure. *Front. Psychol.* 5:387. doi: 10.3389/fpsyg.2014.00387

Stein, T., Sterzer, P., and Peelen, M. V. (2012). Privileged detection of conspecifics: evidence from inversion effects during continuous flash suppression. *Cognition* 125, 64–79. doi: 10.1016/j.cognition.2012.06.005

Sterzer, P., Haynes, J. D., and Rees, G. (2008). Fine-scale activity patterns in high-level visual areas encode the category of invisible objects. *J. Vis.* 8:10. doi: 10.1167/8.15.10

Sterzer P, Stein T, Ludwig K, Rothkirch M and Hesselmann G (2014). Neural processing of visual information under interocular suppression: a critical review. *Front Psychol.* 5:453. doi: 10.3389/fpsyg.2014.00453

Stuit, S. M., Paffen, C. L., van der Smagt, M. J., and Verstraten, F. A. (2011). Suppressed images selectively affect the dominant percept during binocular rivalry. *J. Vis.* 11, pii 7. doi: 10.1167/11.10.7

Stuit, S. M., Verstraten, F. A., and Paffen, C. L. (2010). Saliency in a suppressed image affects the spatial origin of perceptual alternations during binocular rivalry. *Vision Res.* 50, 1913–1921. doi: 10.1016/j.visres.2010.06.014

Tong, F. (2001). Competing theories of binocular rivalry: a possible resolution. *Brain Mind* 2, 55–83. doi: 10.1023/A:1017942718744

Tong, F., Nakayama, K., Vaughan, J. T., and Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron* 21, 753–759. doi: 10.1016/S0896-6273(00)80592-9

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Tsuchiya, N., Koch, C., Gilroy, L. A., and Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *J. Vis.* 6, 1068–1078. doi: 10.1167/6.10.6

Tsuchiya, N., Moradi, F., Felsen, C., Yamazaki, M., and Adolphs, R. (2009). Intact rapid detection of fearful faces in the absence of the amygdala. *Nat. Neurosci.* 12, 1224–1225. doi:10.1038/nn.2380

Vecera, S. P., and Johnson, M. H. (1995). Gaze detection and the cortical processing of faces: evidence from infants and adults. *Vis. Cogn.* 2, 59–87. doi: 10.1080/13506289508401722

Wade, N. J., and Wenderoth, P. (1978). The influence of colour and contour rivalry on the magnitude of the tilt after-effect. *Vision Res.* 18, 827–835. doi: 10.1016/0042-6989(78)90123-2

Wang, L., Weng, X., and He, S. (2012). Perceptual grouping without awareness: superiority of kanizsa triangle in breaking interocular suppression. *PLoS ONE* 7:e40106. doi: 10.1371/journal.pone.0040106

Weiskrantz, L. (1997). *Consciousness Lost and Found: A Neuropsychological Exploration.* New York: Oxford University Press.

White, K. D., Petry, H. M., Riggs, L. A., and Miller, J. (1978). Binocular interactions during establishment of McCollough effects. *Vision Res.* 18, 1201–1215. doi: 10.1016/0042-6989(78)90105-0

Wilson, H. R., Blake, R., and Lee, S. H. (2001). Dynamics of travelling waves in visual perception. *Nature* 412, 907–910. doi: 10.1038/35091066

Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Res.* 24, 471–478. doi: 10.1016/0042-6989(84)90044-0

Yang, E., and Blake, R. (2012). Deconstructing continuous flash suppression. *J. Vis.* 12, 8. doi: 10.1167/12.3.8

Yang, E., Zald, D. H., and Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion* 7, 882–886. doi: 10.1037/1528-3542.7.4.882

Yang, Y. H., and Yeh, S. L. (2011). Accessing the meaning of invisible words. *Conscious. Cogn.* 20, 223–233. doi: 10.1016/j.concog.2010.07.005

Yang, Y. H., and Yeh, S. L. (2014). Unmasking the dichoptic mask by sound: spatial congruency matters. *Exp. Brain Res.* 232, 1109–1116. doi: 10.1007/s00221-014-3820-5

Zadbood, A., Lee, S. H., and Blake, R. (2011). Stimulus fractionation by interocular suppression. *Front. Hum. Neurosci.* 5:135. doi: 10.3389/fnhum.2011.00135

Zhang, P., Jiang, Y., and He, S. (2012). Voluntary attention modulates processing of eye-specific visual information. *Psycho. Sci.* 23, 254–260. doi: 10.1177/0956797611424289

Zhou, G., Zhang, L., Liu, J., Yang, J., and Qu, Z. (2010). Specificity of face processing without awareness. *Conscious. Cogn.* 19, 408–412. doi: 10.1016/j.concog.2009.12.009

Zhou, W., Jiang, Y., He, S., and Chen, D. (2010). Olfaction modulates visual perception in binocular rivalry. *Curr. Biol.* 20, 1356–1358. doi: 10.1016/j.cub.2010.05.059

Zimba, L. D., and Blake, R. (1983). Binocular rivalry and semantic processing: out of sight, out of mind. *J. Exp. Psychol. Hum. Percept. Perform.* 9, 807–815. doi: 10.1037/0096-1523.9.5.807

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 11 February 2014; accepted: 29 April 2014; published online: 23 May 2014.
*Citation: Gayet S, Van der Stigchel S and Paffen CLE (2014) Breaking continuous flash suppression: competing for consciousness on the pre-semantic battlefield. Front. Psychol. **5**:460. doi: 10.3389/fpsyg.2014.00460*
This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

OPINION ARTICLE
published: 06 May 2014
doi: 10.3389/fpsyg.2014.00387

Unconscious processing under interocular suppression: getting the right measure

Timo Stein[1]* and Philipp Sterzer[2,3,4]

[1] Center for Mind/Brain Sciences (CIMeC), University of Trento, Rovereto, Italy
[2] Department of Psychiatry, Charité Universitätsmedizin Berlin, Berlin, Germany
[3] Berlin School of Mind and Brain, Humboldt-Universität zu Berlin, Berlin, Germany
[4] Bernstein Center for Computational Neuroscience, Berlin, Germany
*Correspondence: timo@timostein.de

Edited by:
Julien Dubois, California Institute of Technology, USA

Reviewed by:
Jeroen J. A. Van Boxtel, Monash University, Australia
Kristian Sandberg, Aarhus University Hospital, Denmark

Keywords: unconscious processing, visual awareness, process dissociation, interocular suppression, continuous flash suppression

In order to demonstrate unconscious visual processing, researchers need to select a technique for rendering stimuli invisible and a measure reflecting the processing of these stimuli. The most popular techniques are backward masking, in which the visibility of a very brief stimulus is degraded by the presentation of a succeeding visual pattern (Breitmeyer and Öğmen, 2006), and interocular suppression, where a stimulus shown to one eye degrades the visibility of a stimulus presented to the other eye (Lin and He, 2009). Recently, much work has been carried out using continuous flash suppression (CFS; Tsuchiya and Koch, 2005), a particularly potent interocular suppression technique. In CFS, a train of high-contrast patterns flashed into one eye can suppress the visibility of a stationary stimulus shown to the other eye for up to several seconds (**Figure 1**). Because CFS allows for extended periods of reliable invisibility of complex stimuli, this technique has sparked a surge of interest in unconscious visual processing.

Ideally, research aimed at delineating the scope and limits of visual processing without awareness should adopt the technique that is most sensitive to unconscious processing. This is because a failure to find evidence for a certain unconscious effect could always be due to constraints imposed by the specific technique rather than to the genuine absence of unconscious processing (Faivre et al., 2012). However, since the extent to which a technique allows for unconscious processing is difficult to determine, and due to a lack of general consensus on valid measures of unconscious processing, no definite criteria exist for choosing the most sensitive technique.

CLASSIC DISSOCIATION APPROACHES TO UNCONSCIOUS PROCESSING

Most commonly, unconscious processing is studied using some variant of the classic dissociation paradigm, in which a direct measure of stimulus awareness (e.g., subjective ratings or objective discrimination performance) is contrasted with an indirect measure of stimulus processing (e.g., priming effect). For this comparison to be valid, both measures need to be obtained using identical stimuli and stimulus-response mappings, and the direct task needs to assess awareness of the critical stimulus manipulation that is driving the effect in the indirect measure (Schmidt and Vorberg, 2006). Thus, the only difference between the two measures should lie in the task instructions, with the direct task referring explicitly to the critical stimulus manipulation (Reingold and Merikle, 1988). Schmidt and Vorberg (2006) described three types of dissociations that can provide evidence for unconscious processing, depending on some critical assumptions: (1) The direct measure has null sensitivity while the indirect measure has some sensitivity. This *simple dissociation* requires the direct measure to capture all aspects of relevant conscious perception. (2) The indirect measure has greater sensitivity than the direct measure. This *sensitivity dissociation* requires the direct measure to be at least as sensitive to relevant conscious perception as the indirect measure. (3) Some manipulation has opposite effects on the indirect and the direct measure. Such *double dissociations* may provide the most compelling evidence for the existence of two distinct underlying processes (Mattler, 2003; Vorberg et al., 2003; Lau and Passingham, 2007).

The majority of studies adopting the classic dissociation paradigm followed the simple dissociation logic, probably due to its face validity and practical feasibility. This approach has provided clear evidence for high-level visual and semantic unconscious processing under backward masking (Kouider and Dehaene, 2007; Van den Bussche et al., 2009). Under interocular suppression, by contrast, unconscious processing seems to be comparably limited (Tong et al., 2006; Almeida et al., 2008; Lin and He, 2009). For example, a number of studies have failed to obtain evidence for unconscious processing of facial features rendered invisible through CFS (Moradi et al., 2005; Shin et al., 2009; Yang et al., 2010; Amihai et al., 2011; Stein and Sterzer, 2011; Stein et al., 2012a; but see Adams et al., 2010; Xu et al., 2011; Barbot and Kouider, 2012). This indicates that backward masking represents a more sensitive technique for measuring unconscious high-level processing than interocular suppression.

BREAKING CONTINUOUS FLASH SUPPRESSION (b-CFS)

This notion has recently been challenged by findings obtained with the novel breaking continuous flash suppression (b-CFS)

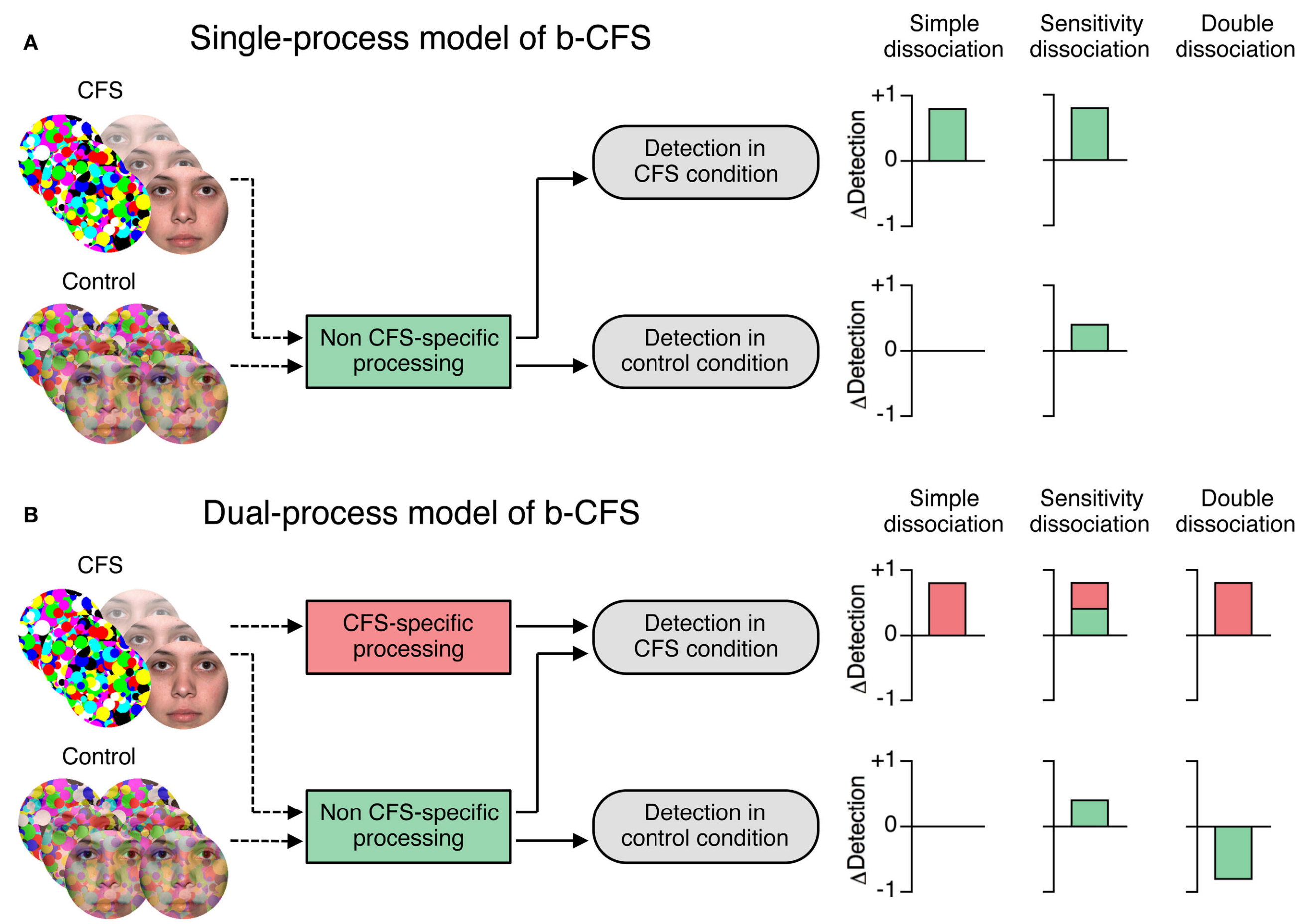


FIGURE 1 | Competing models of the processes mediating detection performance in the b-CFS paradigm. (A) The single-process model posits that both the CFS and the control condition measure differences between stimuli in accessing awareness that exist independent of the application of CFS, i.e., that are caused by *non CFS-specific* processing differences (green boxes and bars). The bar graphs on the right show how the single-process model would account for hypothetical detection differences (ΔDetection in arbitrary units) between two stimuli in the CFS condition (top) and in the control condition (bottom). To account for simple and sensitivity dissociations, the single-process model would need to assume that the CFS condition represents a more sensitive measure of non CFS-specific processing differences than the control condition. The single-process model cannot account for double dissociations. **(B)** The dual-process model posits that differences in conscious detection between stimuli obtained in the CFS condition are at least partly due to the application of CFS, i.e., they reflect *CFS-specific* processing differences (red boxes and bars). In the b-CFS literature, simple and sensitivity dissociations between the CFS and the control condition have been take to support the dual-process model. The dual-process model assumes that CFS-specific processing accounts for effects that are larger in the CFS than in the control condition, as illustrated by the red bar graphs on the right. We, however, suggest that double dissociations between the two conditions (i.e., some experimental manipulation has opposite effects on detection in the CFS and the control condition) are required to refute the single-process model and to postulate distinct CFS-specific processing.

paradigm in which differential unconscious processing during CFS is inferred from the time different stimuli need to overcome CFS and break into awareness, as reflected in speeded localization (or detection) responses (Jiang et al., 2007). A rapidly growing body of literature using b-CFS now suggests that interocular suppression allows for a much greater extent of high-level unconscious processing than previously thought (for a review, see Gayet et al., submitted). For example, b-CFS is sensitive to various features of face stimuli (Jiang et al., 2007; Yang et al., 2007; Zhou et al., 2010; Stein et al., 2011b,c, 2012b, 2014; Chen and Yeh, 2012; Stein and Sterzer, 2012; Stewart et al., 2012; Gobbini et al., 2013a,b), and can even be influenced by semantic stimulus properties (Costello et al., 2009; Mudrik et al., 2011; Sklar et al., 2012). These findings demonstrate that b-CFS is highly sensitive to differences between complex stimuli in their potency to gain access to awareness.

However, detection or localization responses as used in b-CFS represent a measure of conscious stimulus processing. In the classic dissociation paradigm b-CFS would thus count as a *direct* measure of stimulus awareness. Why then is b-CFS typically regarded as a measure of unconscious processing? One possibility is that, because target stimuli in b-CFS remain invisible for up to several seconds, differences in detection time may seem to suggest that the visual system discriminates between stimuli before conscious access, i.e., unconsciously. However, the same logic could in principle be applied to any visual detection measure (Gaillard et al., 2006). Consequently, findings from all experiments measuring visual detection, such as tasks designed as awareness checks, paradigms for measuring contrast detection thresholds, visual search, or attentional blink would need to be reinterpreted as evidence for unconscious processing. Clearly, this interpretation is in direct contradiction to a long history of research into unconscious processing that adopted the classic dissociation logic.

Alternatively, and more likely, is that unconscious processing is inferred from b-CFS only *because* CFS is used to degrade stimulus visibility. That is, differences in access to awareness are attributed to differential processing that occurred specifically under CFS, i.e., to *CFS-specific* processing differences. For this reasoning to be valid, *non CFS-specific* threshold differences need to be ruled out as a cause for differences in access to awareness. To isolate CFS-specific processing, most b-CFS studies contrasted detection performance under CFS with a binocular control condition. This control condition implements the same detection task as the CFS condition, but stimuli are presented binocularly, with the target stimulus gradually blended in on top of the flashing masks. The control condition is intended to capture all non CFS-specific processing differences that could play a role in the CFS condition.

A PROCESS-DISSOCIATION FRAMEWORK FOR b-CFS

Thus, the b-CFS paradigm aims to show a dissociation between the CFS and the control condition in order to provide evidence that CFS-specific processing drives detection performance in the CFS condition. That is, b-CFS studies attempt to refute a single-process model in favor of a dual-process model. The single-process model posits that detection performance in both the CFS and the control condition reflects non CFS-specific processing (**Figure 1A**). By contrast, the dual-process model posits that detection performance in the CFS condition is at least partly mediated by CFS-specific processing (**Figure 1B**). This dissociation logic is markedly different from the classic dissociation paradigm described above, in that both the CFS and the control condition are direct measures that use different stimuli but identical tasks.

To date, b-CFS studies have inferred CFS-specific unconscious processing when an effect was found in the CFS condition but none in the control condition (*simple dissociation*) or when the effect in the CFS condition was larger than in the control condition (*sensitivity dissociation*). These dissociations require the control condition to be at least as sensitive as the CFS condition to all aspects of non CFS-specific processing that might have contributed to the effect in the CFS condition. We have recently shown that this critical assumption is unwarranted, because the CFS and the control condition are not directly comparable and differ in various aspects other than CFS-specific processing (Stein et al., 2011a). Thus, simple or sensitivity dissociations could be due to factors other than CFS-specific processing. In fact, it is possible that the CFS condition is simply a more sensitive measure of non CFS-specific differences in stimulus detectability than the control condition. Hence, simple and sensitivity dissociations cannot provide unequivocal evidence for CFS-specific processing.

However, a *double dissociation* between the CFS and the control condition could be used to directly refute the single-process model. The only assumption required is that non CFS-specific processing differences influence the CFS and the control condition in the same direction. If some experimental manipulation had opposite effects on detection in the CFS and the control condition, this would be inconsistent with the notion that non CFS-specific processing differences were driving the effect in both conditions. Therefore, a dual-process model would be required to fit the data. To illustrate, if an accuracy-based, criterion-free sensitivity measure revealed that under CFS neutral words were detected better than negative words (for response time based evidence, see Yang and Yeh, 2011), whereas in the control condition negative words were detected better than neutral words, this would establish a double dissociation.

Although double dissociations would provide convincing evidence that distinct processes mediate detection in the CFS and the control condition, opposite effects in the CFS and the control condition may be the exception rather than the rule and thus difficult to obtain in practice. Moreover, while double dissociations establish the dissociation of processes, the labels ("conscious" vs. "unconscious") assigned to these processes need to be postulated a priori (Cardoso-Leite and Gorea, 2010). Evidence for a separate process governing detection under CFS would thus not necessarily imply that this process takes place unconsciously. We nevertheless believe that the demonstration of double dissociations is essential for proving the dual-process model of b-CFS and may thus represent the critical first step on the road to a new direct measure of unconscious processing.

OBJECTIVE vs. SUBJECTIVE MEASURES IN b-CFS

Another way of studying unconscious processing that is fundamentally different from the classic dissociation logic is to contrast a direct measure of objective discrimination performance with a direct measure of subjective awareness, such as confidence ratings. On this approach, unconscious processing is inferred when the subjective measure has null sensitivity while the objective measure has some sensitivity (blindsight-like *simple dissociation;* Kolb and Braun, 1995; Kunimoto et al., 2001), or when the objective measure has greater sensitivity than the subjective measure (*sensitivity dissociation;* Sandberg et al., 2011). Following this objective-subjective dissociation logic, future b-CFS studies could collect, on every trial, criterion-free measures of objective and subjective sensitivity rather than response time based detection measures. Dissociations between direct objective and subjective measures would demonstrate unconscious processing and could be compared to the magnitude of objective-subjective dissociations obtained with other psychophysical techniques, such as backward masking (Kanai et al., 2010).

With appropriate stimulus manipulations, objective-subjective dissociations in b-CFS could also be used to probe the extent of unconscious processing. For example, demonstrating greater sensitivity to neutral than negative words in the objective measure (cf. Yang and Yeh, 2011) while showing null sensitivity to both neutral and negative words in the subjective measure could be regarded as evidence for unconscious processing of word meaning. Although the objective-subjective dissociation logic for measuring unconscious processing is still under development and an agreement on a valid, bias-free measure of subjective awareness has yet to be reached (Evans and Azzopardi, 2007; Sandberg et al., 2010; Maniscalco and Lau, 2012; Barrett et al., 2013), we believe that this approach represents a promising future application for b-CFS.

CONCLUSION

For the time being, b-CFS cannot provide evidence for unconscious processing. We therefore suggest that findings from b-CFS that were originally taken as evidence for the processing of "invisible" or "unconscious" stimuli need to be reinterpreted as evidence for differences in mere stimulus detectability. Only studies adopting the well-established classic dissociation paradigm can provide unequivocal evidence for unconscious processing and guide the choice of the most sensitive psychophysical technique for rendering stimuli invisible.

ACKNOWLEDGMENTS

Philipp Sterzer and Timo Stein were supported by the German Research Foundation (grants STE 1430/6-1 and STE 2239/1-1).

REFERENCES

Adams, W. J., Gray, K. L. H., Garner, M., and Graf, E. W. (2010). High-level face adaptation without awareness. *Psychol. Sci.* 21, 205–210. doi: 10.1177/0956797609359508

Almeida, J., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proc. Natl. Acad. Sci. U.S.A.* 105, 15214–15218. doi: 10.1073/pnas.0805867105

Amihai, I., Deouell, L., and Bentin, S. (2011). Conscious awareness is necessary for processing race and gender information from faces. *Conscious. Cogn.* 20, 269–279. doi: 10.1016/j.concog.2010.08.004

Barbot, A., and Kouider, S. (2012). Longer is no better: nonconscious overstimulation reverses priming influences under interocular suppression. *Atten. Percept. Psychophys.* 74, 174–184. doi: 10.3758/s13414-011-0226-3

Barrett, A. B., Dienes, U., and Seth, A. K. (2013). Measures of metacognition on signal-detection theoretic models. *Psychol. Methods* 18, 535–552. doi: 10.1037/a0033268

Breitmeyer, B. G., and Öğmen, H. (2006). *Visual Masking: Time Slices Through Conscious and Unconscious Vision.* Oxford: Oxford University Press. doi: 10.1093/acprof:oso/9780198530671.001.0001

Cardoso-Leite, P., and Gorea, A. (2010). On the perceptual/motor dissociation: a review of concepts, theory, experimental paradigms and data interpretations. *Seeing Perceiving* 23, 89–151. doi: 10.1163/187847510X503588

Chen, Y. C., and Yeh, S. L. (2012). Look into my eyes and i will see you: unconscious processing of human gaze. *Conscious. Cogn.* 21, 1703–1710. doi: 10.1016/j.concog.2012.10.001

Costello, P., Jiang, Y., Baartman, B., McGlennen, K., and He, S. (2009). Semantic and subword priming during binocular suppression. *Conscious. Cogn.* 18, 375–382. doi: 10.1016/j.concog.2009.02.003

Evans, S., and Azzopardi, P. (2007). Evaluation of a bias-free measure of awareness. *Spat. Vis.* 20, 61–67 doi: 10.1163/156856807779369742

Faivre, N., Berthet, V., and Kouider, S. (2012). Nonconscious influences from emotional faces: a comparison of visual crowding, masking, and continuous flash suppression. *Front. Hum. Neurosci.* 3:129. doi: 10.3389/fpsyg.2012.00129

Gaillard, R., Del Cul, A., Naccache, L., Vinckier, F., Cohen, L., and Dehaene, S. (2006). Nonconscious semantic processing of emotional words modulates conscious access. *Proc. Natl. Acad. Sci. U.S.A.* 103, 7524–7529. doi: 10.1073/pnas.0600584103

Gobbini, I., Gors, J. D., Halchenko, Y. O., Hughes, H. C., and Cipolli, C. (2013a). Processing of invisible social cues. *Conscious. Cogn.* 22, 765–770. doi: 10.1016/j.concog.2013.05.002

Gobbini, I., Gors, J. D., Halchenko, Y. O., Rogers, C., Guntupalli, S., Hughes, H., et al. (2013b). Prioritized detection of personally familiar faces. *PLoS ONE* 8:e66620. doi: 10.1371/journal.pone.0066620

Jiang, Y., Costello, P., and He, S. (2007). Processing of invisible stimuli: advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychol. Sci.* 18, 349–355. doi: 10.1111/j.1467-9280.2007.01902.x

Kanai, R., Walsh, V., and Tseng, C. H. (2010). Subjective discriminability of invisibility: a framework for distinguishing perceptual and attentional failures of awareness. *Conscious. Cogn.* 19, 1045–1057. doi: 10.1016/j.concog.2010.06.003

Kolb, F. C., and Braun, J. (1995). Blindsight in normal observers. *Nature* 377, 336–338. doi: 10.1038/377336a0

Kouider, S., and Dehaene, S. (2007). Levels of processing during non-conscious perception: a critical review of visual masking. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 362, 857–875. doi: 10.1098/rstb.2007.2093

Kunimoto, C., Miller, J., and Pashler, H. (2001). Confidence and accuracy of near-threshold discrimination responses. *Conscious. Cogn.* 10, 294–340. doi: 10.1006/ccog.2000.0494

Lau, H., and Passingham, R. E. (2007). Unconscious activation of the cognitive control system in the human prefrontal cortex. *J. Neurosci.* 27, 5805–5811. doi: 10.1523/JNEUROSCI.4335-06.2007

Lin, Z., and He, S. (2009). Seeing the invisible: the scope and limits of unconscious processing in binocular rivalry. *Prog. Neurobiol.* 87, 195–211. doi: 10.1016/j.pneurobio.2008.09.002

Maniscalco, B., and Lau, H. (2012). A signal detection theoretic approach for estimating metacognitive sensitivity from confidence ratings. *Conscious. Cogn.* 21, 422–430. doi: 10.1016/j.concog.2011.09.021

Mattler, U. (2003). Priming of mental operations by masked stimuli. *Percept. Psychophys.* 65, 167–187. doi: 10.3758/BF03194793

Moradi, F., Koch, C., and Shimojo, S. (2005). Face adaptation depends on seeing the face. *Neuron* 45, 169–175. doi: 10.1016/j.neuron.2004.12.018

Mudrik, L., Breska, A., Lamy, D., and Deouell, L. Y. (2011). Integration without awareness: expanding the limits of unconscious processing. *Psychol. Sci.* 22, 764–770. doi: 10.1177/0956797611408736

Reingold, E. M., and Merikle, P. M. (1988). Using direct and indirect measures to study perception without awareness. *Percept. Psychophys.* 44, 563–575. doi: 10.3758/BF03207490

Sandberg, K., Bibby, B. M., Timmermans, B., Cleeremans, A., and Overgaard, M. (2011). Measuring consciousness: task accuracy and awareness as sigmoid functions of stimulus duration. *Conscious. Cogn.* 20, 1659–1675. doi: 10.1016/j.concog.2011.09.002

Sandberg, K., Timmermans, B., Overgaard, M., and Cleeremans, A. (2010). Measuring consciousness: is one measure better than the other? *Conscious. Cogn.* 19, 1069–1078. doi: 10.1016/j.concog.2009.12.013

Schmidt, T., and Vorberg, D. (2006). Criteria for unconscious cognition: three types of dissociation. *Percept. Psychophys.* 68, 489–504. doi: 10.3758/BF03193692

Shin, K., Stolte, M., and Chong, S. C. (2009). The effect of spatial attention on invisible stimuli. *Atten. Percept. Psychophys.* 71, 1507–1513. doi: 10.3758/APP.71.7.1507

Sklar, A. Y., Levy, N., Goldstein, A., Mandel, R., Maril, A., and Hassin, R. R. (2012). Reading and doing arithmetic nonconsiously. *Proc. Natl. Acad. Sci. U.S.A.* 109, 19614–19619. doi: 10.1073/pnas.1211645109

Stein, T., Hebart, M. N., and Sterzer, P. (2011a). Breaking continuous flash suppression: a new measure of unconscious processing during interocular suppression? *Front. Hum. Neurosci.* 5:167. doi: 10.3389/fnhum.2011.00167

Stein, T., Peelen, M. V., and Sterzer, P. (2011b). Adults' awareness of faces follows newborns' looking preferences. *PLoS ONE* 6:e29361. doi: 10.1371/journal.pone.0029361

Stein, T., Peelen, M. V., and Sterzer, P. (2012a). Eye gaze adaptation under interocular suppression. *J. Vis.* 12:1. doi: 10.1167/12.7.1

Stein, T., Senju, A., Peelen, M. V., and Sterzer, P. (2011c). Eye contact facilitates awareness of faces during interocular suppression. *Cognition* 119, 307–311. doi: 10.1016/j.cognition.2011.01.008

Stein, T., Seymour, K., Hebart, M. N., and Sterzer, P. (2014). Rapid fear detection relies on high spatial frequencies. *Psychol. Sci.* 25, 566–574. doi: 10.1177/0956797613512509

Stein, T., and Sterzer, P. (2011). High-level face shape adaptation depends on visual awareness: evidence from continuous flash suppression. *J. Vis.* 11, 5. doi: 10.1167/11.8.5

Stein, T., and Sterzer, P. (2012). Not just another face in the crowd: detecting emotional schematic faces during continuous flash suppression. *Emotion* 12, 988–996. doi: 10.1037/a0026944

Stein, T., Sterzer, P., and Peelen, M. V. (2012b). Privileged detection of conspecifics: evidence from inversion effects during continuous flash suppression. *Cognition* 125, 64–79. doi: 10.1016/j.cognition.2012.06.005

Stewart, L. H., Ajina, S., Getov, S., Bahrami, B., Todorov, A., and Rees, G. (2012). Unconscious evaluation of faces on social dimensions. *J. Exp. Psychol. Gen.* 141, 715–727. doi: 10.1037/a0027950

Tong, F., Meng, M., and Blake, R. (2006). Neural bases of binocular rivalry. *Trends Cogn. Sci.* 10, 502–511. doi: 10.1016/j.tics.2006.09.003

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Van den Bussche, E., Van den Noortgate, W., and Reynvoet, B. (2009). Mechanisms of masked priming: a meta-analysis. *Psychol. Bull.* 135, 452–477. doi: 10.1037/a0015329

Vorberg, D., Mattler, U., Heinecke, A., Schmidt, T., and Schwarzbach, J. (2003). Different time courses for visual perception and action priming. *Proc. Natl. Acad. Sci. U.S.A.* 100, 6275–6280. doi: 10.1073/pnas.0931489100

Xu, S., Zhang, S., and Geng, H. (2011). Gaze-induced joint attention persists under high perceptual load and does not depend on awareness. *Vision Res.* 51, 2048–2056. doi: 10.1016/j.visres.2011.07.023

Yang, E., Hong, S.-W., and Blake, R. (2010). Adaptation aftereffects to facial expressions suppressed from visual awareness. *J. Vis.* 10, 24. doi: 10.1167/6.6.1

Yang, E., Zald, D. H., and Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion* 7, 882–886. doi: 10.1037/1528-3542.7.4.882

Yang, Y. H., and Yeh, S. L. (2011). Accessing the meaning of invisible words. *Conscious. Cogn.* 20, 223–233. doi: 10.1016/j.concog.2010.07.005

Zhou, G., Zhang, L., Liu, J., Yang, J., and Qu, Z. (2010). Specificity of face processing without visual awareness. *Conscious. Cogn.* 19, 408–412. doi: 10.1016/j.concog.2009.12.009

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 10 March 2014; accepted: 13 April 2014; published online: 06 May 2014.

*Citation: Stein T and Sterzer P (2014) Unconscious processing under interocular suppression: getting the right measure. Front. Psychol. **5**:387. doi: 10.3389/fpsyg.2014.00387*

This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

REVIEW ARTICLE
published: 19 May 2014
doi: 10.3389/fpsyg.2014.00453

Neural processing of visual information under interocular suppression: a critical review

Philipp Sterzer[1]*, Timo Stein[2], Karin Ludwig[1,3], Marcus Rothkirch[1] and Guido Hesselmann[1]*

[1] Visual Perception Laboratory, Department of Psychiatry and Psychotherapy, Charité Universitätsmedizin, Berlin, Germany
[2] Center for Mind/Brain Sciences, University of Trento, Rovereto, Italy
[3] Department of Psychology, Humboldt-Universität zu Berlin, Berlin, Germany

Edited by:
Julien Dubois, California Institute of Technology, USA

Reviewed by:
Eunice Yang, University of California, Berkeley, USA
Shlomit Yuval-Greenberg, Tel Aviv University, Israel

****Correspondence:***
Philipp Sterzer and Guido Hesselmann, Visual Perception Laboratory, Department of Psychiatry and Psychotherapy, Charité Universitätsmedizin, Campus Charité Mitte, Charitéplatz 1, 10117 Berlin, Germany
e-mail: philipp.sterzer@charite.de; guido.hesselmann@charite.de

When dissimilar stimuli are presented to the two eyes, only one stimulus dominates at a time while the other stimulus is invisible due to interocular suppression. When both stimuli are equally potent in competing for awareness, perception alternates spontaneously between the two stimuli, a phenomenon called binocular rivalry. However, when one stimulus is much stronger, e.g., due to higher contrast, the weaker stimulus can be suppressed for prolonged periods of time. A technique that has recently become very popular for the investigation of unconscious visual processing is continuous flash suppression (CFS): High-contrast dynamic patterns shown to one eye can render a low-contrast stimulus shown to the other eye invisible for up to minutes. Studies using CFS have produced new insights but also controversies regarding the types of visual information that can be processed unconsciously as well as the neural sites and the relevance of such unconscious processing. Here, we review the current state of knowledge in regard to neural processing of interocularly suppressed information. Focusing on recent neuroimaging findings, we discuss whether and to what degree such suppressed visual information is processed at early and more advanced levels of the visual processing hierarchy. We review controversial findings related to the influence of attention on early visual processing under interocular suppression, the putative differential roles of dorsal and ventral areas in unconscious object processing, and evidence suggesting privileged unconscious processing of emotional and other socially relevant information. On a more general note, we discuss methodological and conceptual issues, from practical issues of how unawareness of a stimulus is assessed to the overarching question of what constitutes an adequate operational definition of unawareness. Finally, we propose approaches for future research to resolve current controversies in this exciting research area.

Keywords: visual perception, binocular rivalry, interocular suppression, neuroimaging, consciousness

INTRODUCTION

When two conflicting images are presented to the two eyes, they usually do not merge into a mixture, but rather tend to rival for exclusive perceptual dominance. When both stimuli are equally potent in competing for dominance, such binocular rivalry typically results in perceptual alternations between the two images every few seconds, similar to other bistable perceptual phenomena that occur during viewing of ambiguous visual stimuli such as the Necker cube or ambiguous motion stimuli (Blake and Logothetis, 2002; Sterzer et al., 2009b). Whenever one of the two rivaling images dominates conscious perception, the other respective image is suppressed from conscious awareness for several seconds. This interocular suppression of visual stimuli through binocular rivalry offers a unique opportunity to study neural responses to visual stimuli in the absence of conscious awareness. However, the assessment of awareness during binocular rivalry in its traditional form is complicated by the fact that it relies entirely on the observers' reports about their subjective visual experience. Moreover, dominance of one image and suppression of the other image are not always complete (*piecemeal rivalry*) and transitions between perceptual states occur largely stochastically and are thus unpredictable to both the observer and the experimenter (Blake and Logothetis, 2002). It is therefore, on the basis of subjective reports of perceptual states during conventional binocular rivalry, difficult to reliably determine at which time exactly an image is suppressed and whether it is fully suppressed from awareness.

One variant of binocular rivalry that allows the experimenter to control perceptual dominance at least for brief periods of time is a technique called *flash suppression* (Wolfe, 1984): when one of the two rivaling images is presented first monocularly, followed by binocular presentation of the two images, the image presented first is likely to be suppressed from awareness at the beginning of binocular presentation. A further modification of this technique, *continuous flash suppression* (CFS), can be used to reliably suppress an image for several seconds or even minutes. For CFS, dynamic high-contrast Mondrian-like patterns (also referred to as CFS masks) are flashed to one eye, rendering lower-contrast stimuli presented to the other eye invisible for extended periods of time (Tsuchiya and Koch, 2005). It should be mentioned that it is not yet clear whether CFS should be regarded as a variant of binocular rivalry that induces particularly strong suppression (Shimaoka and Kaneko, 2011), or whether CFS is supported by mechanisms distinct from binocular rivalry (Tsuchiya et al., 2006).

In the following, we critically review research that examined the neural fate of stimulus information that is suppressed from awareness through interocular suppression, with a focus on the neuroimaging literature. In the first section of this article, we discuss methodological problems in the neuroscientific study of unconscious information processing that pose challenges for the interpretation of the neural signals measured in response to suppressed visual stimuli. The second section reviews studies that investigated the processing of suppressed stimuli in early visual cortex and, in particular, the relationship of awareness and attention in early visual processing. The final part of this article is concerned with the processing of suppressed stimuli in higher-level visual areas, highlighting a recent controversy in regard to dissociable roles of ventral and dorsal stream areas in unconscious information processing. We will close by pointing out possible approaches that we think might help to tackle the methodological problems and heterogeneity of findings in future research.

OBJECTIVE VS. SUBJECTIVE MEASURES OF (UN-)AWARENESS

When conducting research on the neural correlates of visual information processing outside awareness, the experimenter has no direct access to the participant's subjective visual experience of the presented stimuli (Malach, 2008; Seth et al., 2008). Thus, the desired correlation between specific conscious contents (e.g., stimulus seen or not seen) and neuronal activity cannot be directly measured. Ultimately, only correlations between behavioral indications of conscious contents (e.g., verbal reports, button presses) and measures of brain states [e.g., functional magnetic resonance imaging (fMRI), electroencephalography (EEG), magnetoencephalography (MEG)] can be investigated (Overgaard, 2006). As a consequence, activity related to conscious contents needs to be disentangled from response-related and all other unrelated neuronal activity (Aru et al., 2012; de Graaf et al., 2012; Frassle et al., 2014). At a more fundamental level, the question of which type of behavioral report classifies as a valid measure of awareness needs to be answered. Not surprisingly, the debate on the optimal measure of conscious vs. unconscious perception has been a long-standing one in the cognitive sciences (Reingold and Merikle, 1990; Merikle and Reingold, 1998; Kunimoto et al., 2001). An important conceptual and methodological aspect of studies investigating visual processing under interocular suppression concerns the assessment of *un*awareness of a stimulus (Snodgrass, 2004; Pessoa, 2005). The fundamental problem with observers' introspective reports regarding their unawareness of a stimulus is that their report critically depends on subjective criteria. Accordingly, the major criticism of introspection has been that subjective reports are generally susceptible to influences of response bias (Eriksen, 1960; Holender, 1986). Especially in the face of weak or noisy signals, observers might show systematically low confidence in a visual discrimination task, which could be falsely interpreted as an absence of awareness even though a trace of awareness was present but not reported (Bjorkman et al., 1993).

In contrast to such *subjective* measures of unawareness, an observer can be regarded as *objectively* unaware when performance in a "forced-choice" task is at chance level. For instance, when participants have to report in which of two successive intervals a target stimulus was presented, or whether the stimulus belonged to category A or B, above chance level performance indicates awareness of the stimulus, whereas performance not significantly different from chance level indicates the absence of awareness. In the examples given above, chance level in the two-alternative forced-choice tasks would be expressed as 50%, or as $d' = 0$, with d' representing the perceptual sensitivity measure within the mathematical framework of signal detection theory widely used in psychophysics (Green and Swets, 1966; Macmillan and Creelman, 1991). A challenge to the purely objective criterion is the conceivable situation in which participants perform above chance in one task, whereas their performance is at chance level in another task related to the same stimulus. For instance, observers can be at chance level in discriminating the orientation of a pattern while being significantly above chance level in discriminating its location (Zadbood et al., 2011; see also Hong and Blake, 2009). When measuring neural signals associated with the presentation of stimuli outside awareness, it is thus important to precisely define which aspects of the stimuli observers are unaware of. Here we argue that chance level performance has to be demonstrated for the same discrimination that constitutes the dimension of interest in concurrent brain activity recordings. For example, when brain responses to supposedly invisible fearful vs. neutral faces are recorded, participants should be at chance in discriminating between fearful and neutral faces (and not in discriminating between, e.g., intact and scrambled faces).

A critical point concerning objective measures of unawareness is the statistical method that is used to prove that performance is "at chance level." For the objective criterion, one needs to assure that the null hypothesis is true. In this case classical statistics – which test how likely it is for the observed data to occur if the null hypothesis were true – are insufficient (Merikle and Daneman, 2000; Schmidt and Vorberg, 2006). If testing the data against 0, using for example a t-test, a p-value smaller than 0.05 implies that the null hypothesis can be rejected with an error probability smaller than 5%. However, a p-value >0.05 does *not* imply that the null hypothesis is true. In that case the test just has no result, that is, the evidence is not sufficient to support a conclusion (Dienes, 2011). Other statistical methods are therefore needed when our goal is to state evidence for the null hypothesis, which is the case when we want to establish chance-level performance as a proof of objective unawareness. Possible solutions are the use of power analyses (Faul et al., 2007), equivalence confidence intervals (Berger and Hsu, 1996; Overgaard et al., 2013), or Bayesian statistics. In Bayesian statistics, the posterior probability of a hypothesis is tested conditional on the observed data and a prior probability. It is thus possible to directly test two hypotheses against each other and – more importantly – compute a probability value for each of these hypotheses, also if one of them is the null hypothesis. For Bayesian statistics, the two hypotheses need to be defined in terms of prior probability distributions, or "priors." The null hypothesis can be defined as a Dirac delta function, i.e., a function in which every x-value is 0 except at 0. The alternative hypothesis should be modeled according to prior empirical or theoretical knowledge, e.g., as a uniform, normal or half-normal distribution (Dienes, in press). The upper and lower bound or the mean and standard deviation of the respective distribution can be inferred from, e.g., a supraliminal experimental condition or previous research. In order to evaluate chance performance individually for each participant, Rouder et al. (2007) suggest to use a "mass-at-chance model," which is based on Bayesian analyses and gives an – albeit conservative – estimation of the probability that a participant's performance is truly at chance level. Irrespective of the application of this model, one of its virtues is that it demonstrates the importance of having enough power for claims of chance performance.

The assessment of unawareness on the basis of objective criteria alone may be overly conservative as it disregards the observer's introspective account and may overestimate conscious perception in cases where forced-choice tasks are contaminated by unconscious processes. In other words, an observer may be erroneously classified as consciously aware of a stimulus in a situation where motor reports are influenced by some unconscious process, resulting in above chance performance despite phenomenal absence of awareness. Above chance performance in a particular task may thus simply show that stimulus information was processed and had an influence on behavior under conditions in which stimulus processing was not accompanied by awareness (Merikle and Daneman, 2000). Dissociations between introspective reports of visual awareness and objective measures of performance ("blindsight") are well-known to occur in cortically lesioned patients (Stoerig, 2006) but can also be observed in neurologically intact participants (Meeres and Graves, 1990; Lau and Passingham, 2006; Schwiedrzik et al., 2011). It may thus be helpful to complement the objective assessment of unawareness with the concomitant use of subjective measures, especially because subjective reports can provide a trial-by-trial measure of awareness while objective measures indicate observer's overall performance in a particular task. One frequently used subjective behavioral report is to let participants directly rate the visibility of the stimulus on a larger (Sergent and Dehaene, 2004) or smaller scale (Ramsoy and Overgaard, 2004). Characteristic of the latter, the 4-point perceptual awareness scale, is its lack of symmetry, because there is only one "invisible" rating as opposed to three different "visible" ratings, ranging from "weak glimpse" and "almost clear" to "absolutely clear." An alternative and widely applied approach to measure awareness is based on metacognitive (second-order) judgments in the form of confidence ratings. Participants have to indicate their confidence about how accurate their first-order perceptual judgment was (Dienes et al., 1995). For example, participants may be instructed to provide confidence ratings about how well they performed in a preceding stimulus localization task (Rothkirch et al., 2012). Another recently introduced variation on confidence ratings is post-decision wagering, in which confidence levels are expressed in terms of the amount of money the participants are willing bet on their judgments. Presumably, this leads to a higher motivation to reveal all conscious knowledge for the sake of cash rewards (Persaud et al., 2007). However, this approach has also sparked criticism, since wagering behavior is likely biased by subjects' propensity to avoid losses (Schurger and Sher, 2008; Fleming and Dolan, 2010). Although many current researchers would agree that participants' introspective phenomenal reports need to be taken seriously by any study of consciousness (Dehaene and Naccache, 2001), the question of which subjective measure is best suited for a given experimental situation remains a matter of ongoing research and debate (Dienes and Seth, 2010; Sandberg et al., 2010; Szczepanowski et al., 2013). One way to overcome the potential confounding factor of response bias is the implementation of signal detection theory in the analysis of subjective reports by calculating a measure of second-order sensitivity ("type-2" d' as opposed to "type-1" d' based on first-order reports), which is independent of response bias or of where participants place their criterion for making high- and low-confidence judgments (Kunimoto et al., 2001; Szczepanowski and Pessoa, 2007; Kanai et al., 2010).

PROCESSING OF SUPPRESSED VISUAL STIMULI IN EARLY VISUAL CORTEX

Human primary visual cortex (V1) constitutes the first cortical processing stage for the largest part of visual signals from the retina. fMRI studies have consistently shown a tight link between stimulus awareness during binocular rivalry and blood-oxygen level dependent (BOLD) activity levels in V1, with invisible stimuli resulting in much reduced activity levels (Polonsky et al., 2000; Tong and Engel, 2001; Haynes et al., 2005; Lee et al., 2005; Wunderlich et al., 2005). However, this set of findings has recently been challenged by a study that aimed to separate the effects of top-down attention and visual awareness on the BOLD signal in human V1 (Watanabe et al., 2011). Based on the notion that attention and awareness are two dissociable processes supporting distinct functions in the visual system (Lamme, 2003; Koch and Tsuchiya, 2007; van Boxtel et al., 2010, but see Cohen et al., 2012), the authors modulated awareness and attention independently of each other in a 2 × 2 factorial design. They used a variant of CFS in which the mask and the target stimulus overlapped only partially, allowing them to isolate target- from mask-related fMRI-BOLD activity in retinotopic V1. Awareness was modulated by presenting mask and target either to the same eye (visible) or to the two eyes separately (invisible). At the same time, visual attention was manipulated by having participants either report the visibility of the target (attended) or perform a demanding letter detection task at fixation (unattended). Replicating a well-established finding from previous work, the authors found stronger target-related V1 responses when the target stimulus was attended in comparison to the unattended condition (Gandhi et al., 1999; Kastner et al., 1999; Martinez et al., 1999), independent of visibility (also see Bahrami et al., 2007, for the effect of attentional load under CFS). In sharp contrast to earlier fMRI results, however, the authors failed to detect stronger V1 activity to visible than to invisible targets (**Figure 1**). Watanabe et al. (2011) concluded that the previously reported awareness modulation on

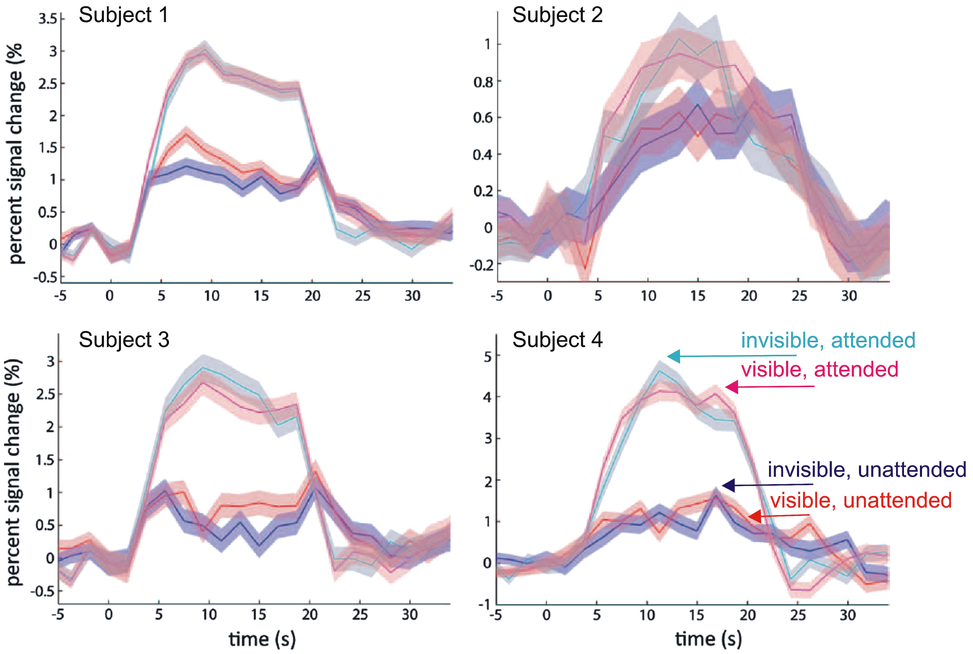


FIGURE 1 | Modulation of fMRI-BOLD activation in primary visual cortex (V1) by attention and visibility. Data from Watanabe et al. (2011): Disc-shaped moving target gratings were rendered invisible by non-overlapping CFS masks. Plotted are time courses of averaged BOLD responses (% change) and 95% confidence intervals in the targeted monocular region from four subjects. The data show a modulation by attention (as operationalized by task at fixation), but no modulation by visibility (cyan: invisible attended; magenta: visible attended; blue: invisible unattended; red: visible unattended). Modified with permission from Watanabe et al. (2011; copyright 2011 The American Association for the Advancement of Science).

the BOLD signal in V1 might be an artifact caused by the concurrent attentional modulation, and that this could also explain the discrepancy between fMRI studies and single-unit recordings that did not find robust awareness-related changes in firing rates of V1 neurons (Leopold and Logothetis, 1996; Wilke et al., 2006).

A recently published study casts doubt on this interpretation. Using a very similar stimulus design and attentional manipulation, but with substantially greater statistical power, Yuval-Greenberg and Heeger (2013) did find a significant modulation of target-evoked V1 activity by CFS. When the mask and target were presented dichoptically and the target was suppressed from awareness, V1 activity was at the same level as during presentation of the CFS mask alone; presentation of mask and target to the same eye, however, resulted in target visibility and was associated with significantly greater BOLD activity levels in V1 (**Figure 2**). Interestingly, a similar difference between presentation to same and different eyes of mask and target was also observed for targets with higher contrast that were not fully suppressed from awareness by CFS. The authors concluded that the presence of the CFS mask may suppress neural activity in V1 similar to other forms of visual masking, suggesting that CFS impacts awareness by modulating the gain of neural responses to the target at an early stage of visual processing. Why did Watanabe et al. (2011) in their earlier study using a similar stimulus design fail to find a modulation of V1 BOLD responses by CFS? As Yuval-Greenberg and Heeger (2013) argue, the study by Watanabe et al. (2011) may have been "underpowered," as they performed only 6–9 experimental runs with just one single trial of 16 s duration per condition in each run, which by current standards in fMRI research is a surprisingly small number of trials indeed. Moreover, the awareness assessment during scanning, in which participants had to distinguish between visible and invisible targets, does not rule out residual visibility even in the "invisible" condition. Participants may have adopted the strategy to label clearly visible targets as visible and less clearly visible targets as invisible, so there is no sufficient proof of target unawareness in the "invisible" condition. (Note that Yuval-Greenberg and Heeger (2013) avoided this issue by including "CFS mask only" trials.) Finally, there were two visible stimulus presentations interspersed in each invisible block (and *vice versa*). These "catch trials" could have attenuated possible BOLD activity differences between visible and invisible blocks.

Given these methodological limitations, the null result regarding V1 activity modulation by CFS reported by Watanabe et al. (2011) cannot be taken as conclusive evidence for the absence of interocular suppression effects in early visual cortex. This conclusion is supported by Yuval-Greenberg and Heeger's (2013) recent study that provided convincing evidence for a V1 BOLD activity modulation by CFS. However, it is still noteworthy that this modulation is relatively subtle, not only relative to the attention-related modulation observed by Watanabe et al. (2011), but also when compared across studies to the strong CFS-related modulation of BOLD responses to object stimuli in higher-level cortex that are discussed in detail in the next section of this article (Fang and He, 2005; Sterzer et al., 2008; Hesselmann

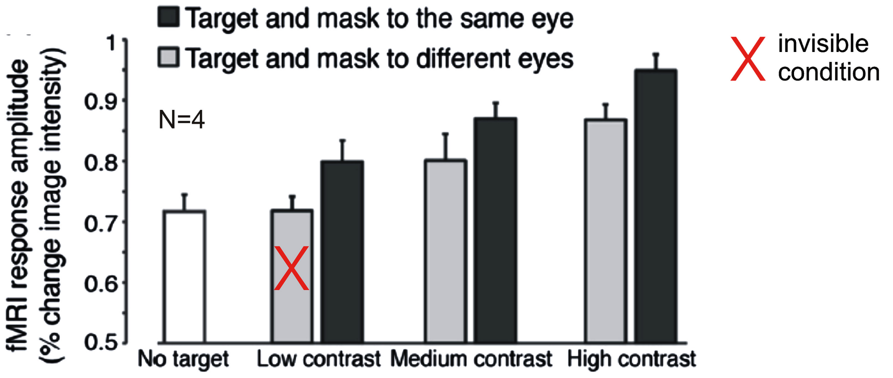


FIGURE 2 | Modulation of fMRI-BOLD activation in primary visual cortex (V1) by contrast and visibility under inattention. Data from Yuval-Greenberg and Heeger (2013): Disc-shaped moving target gratings were rendered invisible by non-overlapping CFS masks. Plotted are average BOLD responses (% change) from four subjects. Gray bars indicate trials with target and masks presented to different eyes, black bars indicate trials with target and masks presented to the same eye. The white bar indicates trials with no target ("CFS mask only"). At low target contrast, interocular suppression (different eyes) rendered targets invisible. The data show a modulation by visibility and contrast, even though subjects were engaged in a task at fixation. Modified with permission from Yuval-Greenberg and Heeger (2013; copyright 2013 Society for Neuroscience).

and Malach, 2011; Hesselmann et al., 2011). This observation is relevant for the discrepancy between electrophysiological recordings in monkeys and human fMRI studies that differed in their conclusions regarding the effects of interocular suppression in low-level visual areas (for an in depth discussion see, Tong et al., 2006; Maier et al., 2008). Single unit recordings showed percept-related changes in firing rates in only ~20% of V1/V2 neurons (Leopold and Logothetis, 1996; Keliris et al., 2010). In contrast fMRI studies found much stronger percept-related V1 BOLD signal modulations during binocular rivalry (Polonsky et al., 2000), sometimes even equivalent to those evoke by stimulus changes (Tong and Engel, 2001; Wunderlich et al., 2005, but see Haynes et al., 2005 who found that BOLD signal modulation during rivalry amounted to only 28% of that evoked by stimulus changes). It is indeed possible that the strong rivalry-related BOLD signal modulations reported in these studies are in large part due to concurrent attentional modulation, as suggested by Watanabe et al. (2011). Alternatively, the discrepancy between monkey neurophysiology and human fMRI studies may simply reflect differences in the nature of the measured signals, with V1 spiking activity being less indicative of conscious perception under interocular suppression than V1 low-frequency local-field potentials (Wilke et al., 2006) and V1 BOLD signals (Maier et al., 2008).

THE FATE OF SUPPRESSED VISUAL INFORMATION BEYOND EARLY VISUAL CORTEX

Early neuroimaging work showed that in high-level extrastriate visual areas the amplitudes of percept-related fMRI signal fluctuations during binocular rivalry are similar to those during actual stimulus alternations (Tong et al., 1998). This finding was initially interpreted as evidence for a resolution of rivalry at early levels through competitive interactions between monocular channels in lateral geniculate nucleus (LGN) and V1, with no maintained representation of the suppressed stimulus at higher levels of the visual processing hierarchy. However, behaviorally the involvement of perceptual (rather than purely interocular) mechanisms is shown by persistence of rivalry when the monocular images are rapidly swapped between the eyes, preventing interocular competition (Logothetis et al., 1996). An influence of perceptual mechanisms is also suggested by the observation that complementary patchworks of intermingled images presented to each eye can drive rivalry (Kovacs et al., 1996). Moreover, binocular rivalry is affected by complex information, such as object category, contained in suppressed stimuli (e.g., Andrews and Blakemore, 1999; Alais and Parker, 2006; see also Blake and Logothetis, 2002; Tong et al., 2006, for reviews), indicating that information from interocularly suppressed stimuli is still processed at sufficiently advanced levels where this information can be extracted and represented.

Recent neuroimaging work has explicitly asked whether complex stimulus information is still represented at advanced stages of the visual processing hierarchy during binocular rivalry suppression, focusing mainly on two questions: first, is visual information that is of special behavioral relevance still processed under interocular suppression? This question is based on the assumption that stimuli of special behavioral relevance, e.g., emotional information (for reviews, see Pessoa, 2005; Vuilleumier, 2005), may undergo preferential and automatic processing in the absence of attention and even awareness. Second, is complex stimulus information such as object category, no matter whether it is of particular behavioral relevance, represented in functionally specialized high-level visual areas during suppression? And in particular, are there differences between such high-level visual areas, e.g., ventral and dorsal stream areas, regarding the degree to which suppressed information is processed?

PROCESSING OF EMOTIONALLY AND SOCIALLY RELEVANT INFORMATION UNDER INTEROCULAR SUPPRESSION

With regard to the question whether emotional information is processed during interocular suppression, results from fMRI studies consistently indicate enhanced processing of emotional facial expressions. Williams et al. (2004) presented either faces with neutral, happy, or fearful expressions to one eye and houses to the other eye. Stimuli were presented only for a short, fixed duration and the contrast and hue of the rivalrous images was manipulated so that just one image class was reliably perceived while the other image was suppressed. Activation in the fusiform face area (FFA) and parahippocampal place area (PPA) was increased for perceptually dominant versus suppressed faces and houses. In contrast, amygdala activation was increased in response to fearful versus neutral faces regardless of whether the face was dominant or suppressed, in line with the view that detection of emotional information proceeds automatically and does not require awareness (Vuilleumier, 2005). Similarly, during rivalry between a fearful face or a chair stimulus shown to one eye and a house stimulus (that was moving in order to ensure its dominance) to the other eye, activity in the amygdala was greater in response to suppressed fearful faces compared to chairs (Pasley et al., 2004). No such response difference was observed in ventral visual cortex in this study, from which the authors concluded that a high-level cortical representation is not required for the discrimination of certain behaviorally relevant stimuli in the amygdala. However, a more recent study in which fearful faces or houses were suppressed by moving checkerboards found stronger responses to fearful faces than to houses not only in the left amygdala, but also in left FFA (Troiani et al., 2012, but see Troiani and Schultz, 2013 for a failure to replicate these findings using CFS with high-contrast Mondrian-like masks).

It should be noted, however, that in the binocular rivalry studies mentioned above unawareness of the suppressed image was assessed either by using a one-back task that required participants to report repetitions of identical face or house stimuli (Williams et al., 2004), or by instructing participants to press a button if at any point they perceived anything else but the dominant house, checkerboard, or Mondrian-like stimulus (Pasley et al., 2004). As such methods do not reliably ensure objective unawareness of the suppressed stimuli, it cannot be ruled out that the observed response differences for suppressed faces might have been at least in part due to residual traces of stimulus awareness that went undetected by the tasks used.

In another fMRI study, CFS was used to render faces with fearful or neutral expressions invisible (Jiang and He, 2006). Here, a forced-choice task was used at least in behavioral pre- and post-scan sessions and showed that observers were unable to discriminate between suppressed intact and scrambled face stimuli, in addition to a subjective awareness assessment during fMRI scanning. Responses to invisible face stimuli in the FFA were strongly reduced relative to visible faces, but did not show differences between neutral and fearful expressions. In contrast, greater responses to fearful than to neutral faces were observed in the amygdala and in the superior temporal sulcus (see also Vizueta et al., 2012), a region previously implicated in the processing of changeable facial features such as expression or eye gaze (Haxby et al., 2000). In a subsequent EEG study from the same group (Jiang et al., 2009), the amplitude of the N170, a face-specific signal thought to reflect face processing in ventral occipitotemporal cortex, was not significantly different for fearful and neutral faces. In contrast, a later signal along the superior temporal sulcus was specific for fearful expressions. Further support for the notion that changeable facial features of particular social relevance might be processed without awareness along specialized neural pathways comes from a recent EEG study that found larger negative deflections at parietofrontal electrodes to suppressed faces with direct gaze compared to suppressed faces with averted gaze (Yokoyama et al., 2013). Although still exploratory, this finding is in line with behavioral evidence of unconscious processing of eye gaze under interocular suppression (Stein et al., 2011b, 2012; Xu et al., 2011; Chen and Yeh, 2012).

Together, neuroimaging studies of emotional face processing provide little evidence for processing of the category or the emotional information of suppressed object stimuli in high-level ventral visual areas such as the FFA. In contrast, both the amygdala and superior temporal sulcus show differential responses to suppressed fearful and neutral face stimuli. This is consistent with the notion of automatic processing of threat-signaling stimuli (Vuilleumier, 2005), which has been suggested to bypass the visual processing stages at which binocular conflict is resolved, possibly via subcortical pathways (LeDoux, 2000). Indeed, some fMRI studies provided indirect support for a role of subcortical pathways in driving amygdala activity to suppressed fearful faces by showing covarying activity between the amygdala and other visually responsive subcortical structures such as the superior colliculus (Pasley et al., 2004) and the pulvinar (Troiani et al., 2012; Troiani and Schultz, 2013). However, recent recordings from a depth electrode implanted in a patient's amygdala revealed that responses to fearful faces rendered invisible through CFS occur only relatively late, after about 140 ms, and are driven by both low and high spatial frequencies in the facial stimuli (Willenbockel et al., 2012). These findings are inconsistent with the notion of a direct feedforward connection between the superior colliculus, pulvinar, and the amygdala, as this pathway is assumed to be particularly fast and to rely exclusively on low spatial frequency information. Similarly, a recent behavioral study has shown that privileged processing of threat-signaling visual stimuli does not rely on low spatial frequencies (Stein et al., 2014), again challenging the idea of a subcortical fast track for emotionally relevant visual information (for an in-depth discussion, see Pessoa and Adolphs, 2010). Clearly, more work is needed to pinpoint the neural networks underlying unconscious processing of emotionally charged and socially significant stimuli under rivalry suppression.

OBJECT- AND CATEGORY-SPECIFIC PROCESSING IN HIGH-LEVEL AREAS OF THE DORSAL AND THE VENTRAL STREAM

The other question that has been addressed by a number of recent neuroimaging studies is whether complex stimulus information regarding object identity or category can also survive suppression at early stages and be retained at advanced stages of visual processing. Importantly, just the absence of evidence for category-specific processing in specialized ventral visual areas during suppression (Pasley et al., 2004; Williams et al., 2004) cannot be taken as definite proof for the absence of such processing, as weak residual neural signals evoked by suppressed stimuli may have gone undetected by the neuroimaging methods used. Fang and He (2005) investigated neural responses to object stimuli suppressed by CFS in high-level areas pertaining to the ventral and dorsal streams of visual processing, respectively. Their stimuli included images of faces, which evoke mostly ventral activity, and images of tools, for which a dorsal preference has been shown. Similar to the above-mentioned studies (Pasley et al., 2004; Williams et al., 2004), they did not observe any category-specific fMRI responses to invisible images of faces or tools in ventral visual areas. In contrast, dorsal regions did show responses to suppressed stimuli that were much less reduced in amplitude relative to visible stimuli (**Figure 3**), but exclusively for images of tools. The authors concluded that indeed substantial information from the suppressed eye could escape competitive interactions at early processing levels and reach dorsal visual areas, but not ventral areas. In line with previous evidence from lesion studies in humans and from animal studies (Milner and Goodale, 1995, 2006), they interpreted these findings as support for a fundamental specialization of the visual system into a dorsal *vision-for-action* stream and a ventral *vision-for-perception* stream. According to this theory, dorsal areas form action-relevant representations for selected types of visual objects, e.g., tools and other man-made manipulable objects, even in the absence of awareness, while there are no such representations in ventral visual areas.

Findings from subsequent neuroimaging studies have provided partly diverging evidence that has questioned these conclusions. Using high-resolution fMRI study and multi-voxel pattern analysis to increase the sensitivity for distributed fMRI signals (Haynes and Rees, 2006; Norman et al., 2006) the fine-grained spatial activity patterns within the ventral areas FFA and PPA were shown to still contain information about the category of face and house stimuli even when the average BOLD signal was drastically reduced and stimuli were reliably suppressed from conscious perception, as evidenced by a rigorous objective awareness assessment during fMRI scanning (**Figures 4A,B**; Sterzer et al., 2008). Thus, the fine-grained spatial pattern of activity measured with fMRI in ventral visual areas encodes information about the identity of suppressed object stimuli. Similarly, face-specific electromagnetic responses to interocularly suppressed stimuli are reduced in amplitude but still present in the human ventral visual pathway (Sterzer et al., 2009a). These results are consistent with more general findings of high-level processing for stimuli outside awareness in other paradigms (e.g., see Kouider and Dehaene, 2007; Rees, 2007). Such unconscious high-level processing could provide a neural basis for how complex stimulus features contribute to the resolution of perceptual conflict even when suppressed (e.g., by high-level adaptation). The processing of suppressed stimuli, however, does not seem to extend to semantic information (i.e., semantic congruency between lexical units), as a recent EEG study found signals related to the semantic mismatch between two words (the N400) to be absent when participants could not discriminate the meaning of suppressed words (Kang et al., 2011).

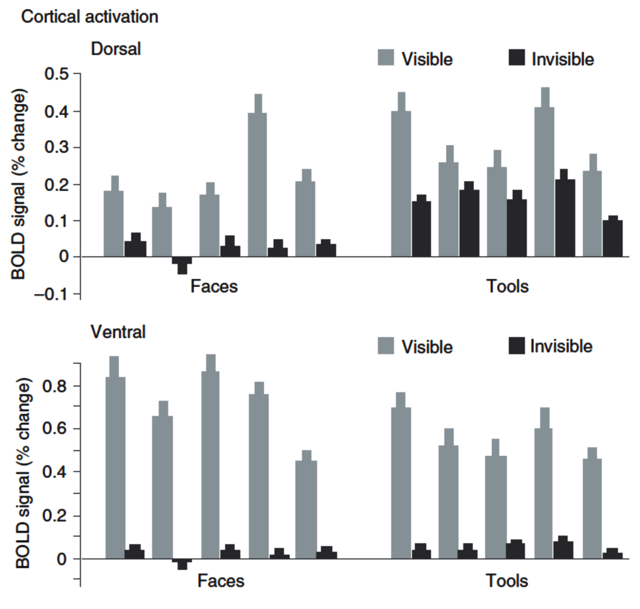


FIGURE 3 | fMRI-BOLD activation to visual stimuli suppressed by CFS. Data from Fang and He (2005): Plotted are BOLD signals (% change) in dorsal and ventral stream to visible and invisible images of tools and faces. The ventral stream shows a strong reduction of activity under CFS, while the dorsal stream shows much less reduction when images are tools. Shown are data from five participants. Reproduced from Fang and He (2005; copyright 2005 Nature Publishing Group).

A recently published study also questioned the distinction between dorsal and ventral visual areas in the processing of suppressed object stimuli (Hesselmann and Malach, 2011). In this study participants had to detect, during CFS, images of tools. Despite their substantial difference in connectivity and neuroanatomical specialization, both ventral and dorsal stream areas revealed a similarly tight link to perceptual awareness, that is, strong fMRI signals for visible tools but a significant reduction of activity in the invisible condition (**Figure 4C**). In other words, this study failed to replicate the previous finding (Fang and He, 2005) that specifically dorsal areas contain representations of manipulable objects during binocular rivalry suppression. Another interesting observation from this study is that CFS did not lead to a complete abolition of category-specific activity in response to invisible stimuli, as object category could still be decoded from fMRI signal patterns in lateral occipital cortex with multi-voxel pattern analyses (**Figure 4D**), in line with the above-mentioned previous work (Sterzer et al., 2008). The divergent findings between the studies by Fang and He (2005) and Hesselmann and Malach (2011) may be explained by differences in study design, especially with respect to the behavioral assessment of unawareness. In the experiments of Fang and He (2005), participants were asked to report whether they perceived any shape or object after prolonged blocks of fMRI scanning while their task was to detect occasional size changes of the fixation point. Only a subset of participants performed a trial-wise forced-choice task in separate control experiments ("offline") to establish objective absence of awareness. In contrast, Hesselmann and Malach (2011) used a trial-by-trial forced-choice task during the main fMRI experiment ("online"), which constitutes a more direct and arguably more sensitive test for visibility. As high-order visual areas specialized on object processing are very sensitive even to poorly visible low contrast images or object parts (Avidan et al., 2002; Lerner et al., 2002), it cannot be excluded, because of the comparably insensitive assessment of unawareness, that responses to invisible tools in the study by Fang and He (2005) were at least in part due to occasional traces of residual target visibility. However, against this argument of residual but unreported visibility seems to speak the fact that only dorsal but not ventral stream areas showed preserved activity under CFS.

In a further study that focused on the relationship between report type, subjective versus objective, and fMRI responses to face or tool stimuli during CFS, Hesselmann et al. (2011) replicated their previous finding of similar fMRI signal reductions in both ventral and dorsal visual areas when stimuli were invisible. In addition, they showed a dissociation between type of report and low- vs. high-level visual areas: Activity in high-level visual areas was enhanced when subjects reported higher levels of subjective visibility, even when objective performance was constant. In contrast, with constant subjective performance, these areas showed no activity differences between trials with objectively correct or incorrect responses. On the other hand, objective behavioral performance was linked to the accuracy of multivariate pattern classification mainly in early visual areas, thus suggesting that subjective and objective reports tap cortical signals of different location and amplitude within the visual cortex (Hesselmann et al., 2011).

In summary, neuroimaging studies investigating the processing of visual information during interocular suppression have shown repeatedly that object- or category-specific neural activity in high-level visual areas of the ventral stream is strongly reduced, but can be retrieved when sufficiently sensitive methods of data analysis are used, such as multi-voxel pattern analysis of fMRI data. It will be an important challenge for future research to determine to what degree such residual traces of object-related neural activity are relevant behaviorally, e.g., in that they influence the access of object information to awareness (see below). Research into a putative dissociation of ventral and dorsal stream areas in the processing of object information has not provided conclusive results yet. Possibly, dorsal areas are more sensitive than ventral areas to the presence of weak or noisy information, but responses in dorsal and ventral areas seem to be reduced to a similar degree

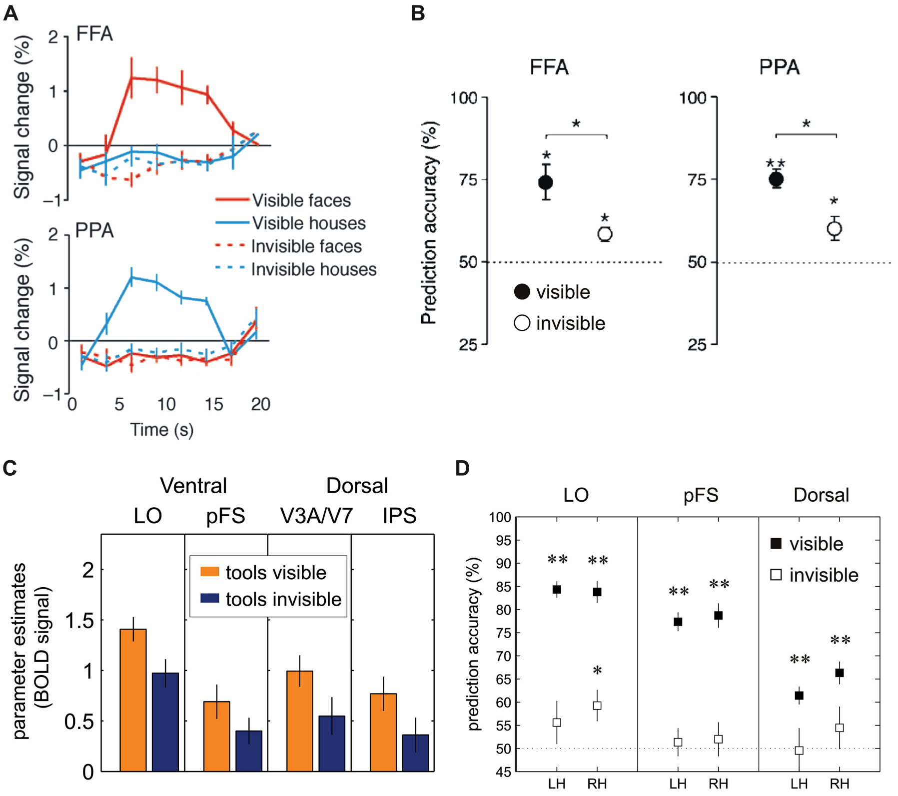


FIGURE 4 | Univariate and multivariate analysis of FMRI-BOLD activation to visual stimuli suppressed by CFS. (A) Sterzer et al. (2008): The fusiform face area (FFA) and the parahippocampal place area (PPA) in inferior temporal cortex showed significantly reduced BOLD activity levels whenever images of faces or houses were rendered invisible. **(B)** Sterzer et al. (2008): Performance of support-vector-machine (SVM) classifiers for pairwise classification of face and house presentations from FFA and PPA. Filled circles: visible trials; open circles: invisible trials. **(C)** Hesselmann and Malach (2011): BOLD signals (parameter estimates in arbitrary units) to images of tools in dorsal and ventral visual areas show stream-invariant reduction whenever stimuli were rendered invisible (LO = lateral occipital area, pFS = posterior fusiform gyrus, IPS = intra-parietal sulcus). **(D)** Hesselmann and Malach (2011): Performance of SVM classifiers in left hemisphere (LH) and right hemisphere (RH) dorsal and ventral visual areas. Prediction accuracies in visible trials (filled squares) were significant in all regions-of-interest; in invisible trials (open squares), area LO showed classification performance significantly above chance level ($*p < 0.01$; $**p < 0.001$). **(A,B)** Reproduced from Sterzer et al. (2008; copyright 2008 Association for Research in Vision and Ophthalmology). **(C,D)** Modified from Hesselmann and Malach (2011; copyright 2011 Oxford University Press).

when object stimuli are fully and objectively suppressed from awareness.

CURRENT CHALLENGES AND FUTURE DIRECTIONS

As outlined in this review, neuroimaging studies of interocular suppression have provided important new insights into unconscious visual information processing, but also generated new controversies. When trying to draw a coherent picture of the neural events that are related to the processing of visual information under interocular suppression, one of the major challenges at the current stage is the heterogeneity of findings. This is the case both when we ask whether a given neural structure is involved in processing of suppressed stimuli at all, but also when it comes to the question of feature- or category-specific processing in the absence of awareness. At least some of the inconsistencies between studies may be related to differences in the depth of interocular suppression. There are in principle two scenarios that could account for heterogeneous findings on the basis of suppression depth: In the first scenario, suppression is not deep enough and the stimulus breaks through and is partially or even fully visible, at least from time to time. If awareness is not assessed stringently on a trial-to-trial basis, this could result in false-positive findings and the erroneous conclusion that neural processing is preserved in the absence of awareness in cases where in fact it is not. In the second scenario, suppression could be too deep, thereby fully abolishing neural responses that could in principle still occur in the absence of awareness. Such a scenario could result in false-negative conclusions. Future studies should aim at avoiding both these scenarios by taking great care in defining those conditions under which neural processing of a stimulus is not unnecessarily deadened despite reliable suppression from awareness. Promising approaches could be to systematically vary the properties of the mask and/or the target stimulus that are most relevant for the depth of interocular suppression, such as stimulus contrast and spatial frequency (Yang and Blake, 2012), or to adjust the suppression threshold individually to a point where stimulus power is as high as possible but as low as necessary (for suppression to work). As discussed above, careful assessment and documentation of unawareness will be of key importance to any study concerned with neural processing under interocular suppression, as this will help the interpretation of each study's findings as well as the comparison of findings between studies.

A point that has received little attention to date concerns the functional relevance of neural signals that are recorded under conditions of interocular suppression. Are preserved neural responses to suppressed stimuli relevant for behavior, or could they be entirely irrelevant and thus just "epiphenomenal?" To assess the functional relevance of unconscious visual information processing under interocular suppression, many studies have measured how invisible stimuli modulate behavioral responses to a succeeding visible stimulus, adopting priming, adaptation aftereffects, or attentional cueing paradigms (Moradi et al., 2005; Jiang et al., 2006; Almeida et al., 2008, 2013; Stein and Sterzer, 2011; Anderson et al., 2012; Faivre et al., 2012). By using stimuli and tasks of different complexity, such behavioral methods have been used to indirectly infer unconscious neural processing at different levels of the visual hierarchy. What is lacking to date however, are neuroimaging studies that use such behavioral measures concurrently to directly establish the functional relevance of brain signals measured under interocular suppression.

One limitation of the behavioral measures of unconscious processing discussed so far is that they assess effects of suppressed stimuli *after* they have been presented outside awareness. They are therefore limited by the potentially short-lived nature of unconscious effects (Greenwald et al., 1996) and constrained by specific task requirements. So far, only few studies have measured behavioral effects of interocularly suppressed stimuli on-line, that is, *during* the presentation of stimuli outside awareness. One way to do so is to monitor motor behavior related to the invisible stimulus during presentation. A recent study analyzed grasping movements to stimuli that were suppressed from awareness by CFS (Roseboom and Arnold, 2011). The authors found that participants learned to adjust the orientation of their hand to the stimulus orientation over the course of the experiment. In contrast, applying a more rigorous control of stimulus visibility across sessions, another study (Ludwig et al., 2013) failed to find evidence for the use of unconscious stimulus information by the visuomotor system: Participants neither learned to adjust the size of their grip aperture nor the orientation of their hand to invisible stimuli. Thus, whether grasping movements are indeed a useful way of measuring the behavioral effects of unconscious visual processing under interocular suppression awaits further clarification. Possibly, the monitoring of eye movements may prove a more useful approach: Using eye movements as a behavioral response measure, it was recently demonstrated that observers spend more time looking at suppressed stimuli despite being unable to correctly guess the stimulus location in a manual forced-choice task (Rothkirch et al., 2012). Eye movement recordings thus seem to be a promising technique to determine the functional relevance of neural signals recorded during interocular suppression (see also Spering et al., 2011; Spering and Carrasco, 2012, for a dissociation of eye movements and reported perception).

Another technique that has recently become very popular is "breaking-CFS" (b-CFS), which measures the time it takes until a stimulus breaks into awareness after initial suppression through CFS, thus supposedly indicating the strength of neural processing while the stimulus is still suppressed (Jiang et al., 2007). However, whether b-CFS actually reflects unconscious processing is currently a matter of debate (Stein et al., 2011a; Stein and Sterzer, 2014). Neuroimaging studies could help resolving this debate by demonstrating a tight coupling between neural responses to the initially invisible stimulus and the duration of perceptual suppression (Yamashiro et al., 2013). If brain signals during full suppression predicted subsequent breakthrough into awareness on a trial-by-trial basis, this would provide direct evidence for the functional relevance of unconscious neural processing in mediating access to awareness.

Since evidence for functional relevance of neural signals in response to interoculary suppressed stimuli is still sparse, further research is warranted to provide a better understanding of how such unconscious visual information can modulate behavior, and which neural processes might mediate such effects. This is a challenging task, as it requires observers to be unaware of the association between a suppressed stimulus and their own behavior. It also seems crucial to learn more about which behavioral measures are best suited to study behavioral responses under interocular suppression. For instance, continuous behavioral measures might capture neural activity related to suppressed stimuli that is not reflected in discrete measures, such as manual button presses (Fahle et al., 2011; Naber et al., 2011). It remains an intriguing challenge for future research to establish experimental approaches that allow us to explore the functional relevance of neural signals measured in response to visual stimuli during interocular suppression.

ACKNOWLEDGMENTS

Guido Hesselmann, Marcus Rothkirch, Philipp Sterzer and Timo Stein were supported by the German Research Foundation (grants HE 6244/1-1, STE 1430/2-1, STE 1430/6-1, and STE 2239/1-1). Karin Ludwig was supported by the *Studienstiftung des deutschen Volkes* (German National Academic Foundation).

REFERENCES

Alais, D., and Parker, A. (2006). Independent binocular rivalry processes for form and motion. *Neuron* 52, 911–920. doi: 10.1016/j.neuron.2006.10.027

Almeida, J., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proc. Natl. Acad. Sci. U.S.A.* 105, 15214–15218. doi: 10.1073/pnas.0805867105

Almeida, J., Pajtas, P. E., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2013). Affect of the unconscious: visually suppressed angry faces modulate our decisions. *Cogn. Affect. Behav. Neurosci.* 13, 94–101. doi: 10.3758/s13415-012-0133-7

Anderson, E., Siegel, E., White, D., and Barrett, L. F. (2012). Out of sight but not out of mind: unseen affective faces influence evaluations and social impressions. *Emotion* 12, 1210. doi: 10.1037/a0027514

Andrews, T. J., and Blakemore, C. (1999). Form and motion have independent access to consiousness. *Nat. Neurosci.* 2, 405–406. doi: 10.1038/8068

Aru, J., Bachmann, T., Singer, W., and Melloni, L. (2012). Distilling the neural correlates of consciousness. *Neurosci. Biobehav. Rev.* 36, 737–746. doi: 10.1016/j.neubiorev.2011.12.003

Avidan, G., Harel, M., Hendler, T., Ben-Bashat, D., Zohary, E., and Malach, R. (2002). Contrast sensitivity in human visual areas and its relationship to object recognition. *J. Neurophysiol.* 87, 3102–3116.

Bahrami, B., Lavie, N., and Rees, G. (2007). Attentional load modulates responses of human primary visual cortex to invisible stimuli. *Curr. Biol.* 17, 509–513. doi: 10.1016/j.cub.2007.01.070

Berger, R. L., and Hsu, J. C. (1996). Bioequivalence trials, intersection-union tests and equivalence confidence sets. *Stat. Sci.* 11, 283–319. doi: 10.1214/ss/1032280304

Bjorkman, M., Juslin, P., and Winman, A. (1993). Realism of confidence in sensory discrimination: the underconfidence phenomenon. *Percept. Psychophys.* 54, 75–81. doi: 10.3758/BF03206939

Blake, R., and Logothetis, N. K. (2002). Visual competition. *Nat. Rev. Neurosci.* 3, 13–21. doi: 10.1038/nrn701

Chen, Y. C., and Yeh, S. L. (2012). Look into my eyes and I will see you: unconscious processing of human gaze. *Conscious. Cogn.* 21, 1703–1710. doi: 10.1016/j.concog.2012.10.001

Cohen, M. A., Cavanagh, P., Chun, M. M., and Nakayama, K. (2012). The attentional requirements of consciousness. *Trends Cogn. Sci.* 16, 411–417. doi: 10.1016/j.tics.2012.06.013

de Graaf, T. A., Hsieh, P. J., and Sack, A. T. (2012). The 'correlates' in neural correlates of consciousness. *Neurosci. Biobehav. Rev.* 36, 191–197. doi: 10.1016/j.neubiorev.2011.05.012

Dehaene, S., and Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition* 79, 1–37. doi: 10.1016/S0010-0277(00)00123-2

Dienes, Z. (2011). Bayesian versus orthodox statistics: which side are you on? *Perspect. Psychol. Sci.* 6, 274–290. doi: 10.1177/1745691611406920

Dienes, Z. (in press). "How Bayesian statistics are needed to determine whether mental states are unconscious," in *Behavioral Methods in Consciousness Research*, ed. M. Overgaard (Oxford: Oxford University Press).

Dienes, Z., Altmann, G., Kwan, L., and Goode, A. (1995). Unconscious knowledge of artificial grammars is applied strategically. *J. Exp. Psychol. Learn. Mem. Cogn.* 21, 1322–1338. doi: 10.1037/0278-7393.21.5.1322

Dienes, Z., and Seth, A. (2010). Gambling on the unconscious: a comparison of wagering and confidence ratings as measures of awareness in an artificial grammar task. *Conscious. Cogn.* 19, 674–681. doi: 10.1016/j.concog.2009.09.009

Eriksen, C. W. (1960). Discrimination and learning without awareness: a methodological survey and evaluation. *Psychol. Rev.* 67, 279–300. doi: 10.1037/h0041622

Fahle, M. W., Stemmler, T., and Spang, K. M. (2011). How much of the "unconscious" is just pre–threshold? *Front. Hum. Neurosci.* 5:120. doi: 10.3389/fnhum.2011.00120

Faivre, N., Berthet, V., and Kouider, S. (2012). Nonconscious influences from emotional faces: a comparison of visual crowding, masking, and continuous flash suppression. *Front. Psychol.* 3:129. doi: 10.3389/fpsyg.2012.00129

Fang, F., and He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nat. Neurosci.* 8, 1380–1385. doi: 10.1038/nn1537

Faul, F., Erdfelder, E., Lang, A. G., and Buchner, A. (2007). G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav. Res. Methods* 39, 175–191. doi: 10.3758/BF03193146

Fleming, S. M., and Dolan, R. J. (2010). Effects of loss aversion on post-decision wagering: implications for measures of awareness. *Conscious. Cogn.* 19, 352–363. doi: 10.1016/j.concog.2009.11.002

Frassle, S., Sommer, J., Jansen, A., Naber, M., and Einhauser, W. (2014). Binocular rivalry: frontal activity relates to introspection and action but not to perception. *J. Neurosci.* 34, 1738–1747. doi: 10.1523/JNEUROSCI.4403-13.2014

Gandhi, S. P., Heeger, D. J., and Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proc. Natl. Acad. Sci. U.S.A.* 96, 3314–3319. doi: 10.1073/pnas.96.6.3314

Green, D. M., and Swets, J. A. (1966). *Signal Detection Theory and Psychophysics.* New York: Wiley.

Greenwald, A. G., Draine, S. C., and Abrams, R. L. (1996). Three cognitive markers of unconscious semantic activation. *Science* 273, 1699–1702. doi: 10.1126/science.273.5282.1699

Haxby, J. V., Hoffman, E. A., and Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends Cogn. Sci.* 4, 223–233. doi: 10.1016/S1364-6613(00)01482-0

Haynes, J. D., Deichmann, R., and Rees, G. (2005). Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature* 438, 496–499. doi: 10.1038/nature04169

Haynes, J. D., and Rees, G. (2006). Decoding mental states from brain activity in humans. *Nat. Rev. Neurosci.* 7, 523–534. doi: 10.1038/nrn1931

Hesselmann, G., Hebart, M., and Malach, R. (2011). Differential BOLD activity associated with subjective and objective reports during "blindsight" in normal observers. *J. Neurosci.* 31, 12936–12944. doi: 10.1523/JNEUROSCI.1556-11.2011

Hesselmann, G., and Malach, R. (2011). The link between fMRI-BOLD activation and perceptual awareness is "stream-invariant" in the human visual system. *Cereb. Cortex* 21, 2829–2837. doi: 10.1093/cercor/bhr085

Holender, D. (1986). Semantic activation without conscious identification in dichotic listening, parafoveal vision, and visual masking: a survey and appraisal. *Behav. Brain Sci.* 9, 1–23. doi: 10.1017/S0140525X00021269

Hong, S. W., and Blake, R. (2009). Interocular suppression differentially affects achromatic and chromatic mechanisms. *Attent. Percept. Psychophys.* 71, 403–411. doi: 10.3758/APP.71.2.403

Jiang, Y., Costello, P., Fang, F., Huang, M., and He, S. (2006). A gender- and sexual orientation-dependent spatial attentional effect of invisible images. *Proc. Natl. Acad. Sci. U.S.A.* 103, 17048–17052. doi: 10.1073/pnas.0605678103

Jiang, Y., Costello, P., and He, S. (2007). Processing of invisible stimuli: advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychol. Sci.* 18, 349–355. doi: 10.1111/j.1467-9280.2007.01902.x

Jiang, Y., and He, S. (2006). Cortical responses to invisible faces: dissociating subsystems for facial-information processing. *Curr. Biol.* 16, 2023–2029. doi: 10.1016/j.cub.2006.08.084

Jiang, Y., Shannon, R. W., Vizueta, N., Bernat, E. M., Patrick, C. J., and He, S. (2009). Dynamics of processing invisible faces in the brain: automatic neural encoding of facial expression information. *Neuroimage* 44, 1171–1177. doi: 10.1016/j.neuroimage.2008.09.038

Kanai, R., Walsh, V., and Tseng, C. H. (2010). Subjective discriminability of invisibility: a framework for distinguishing perceptual and attentional failures of awareness. *Conscious. Cogn.* 19, 1045–1057. doi: 10.1016/j.concog.2010.06.003

Kang, M. S., Blake, R., and Woodman, G. F. (2011). Semantic analysis does not occur in the absence of awareness induced by interocular suppression. *J. Neurosci.* 31, 13535–13545. doi: 10.1523/JNEUROSCI.1691-11.2011

Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., and Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* 22, 751–761. doi: 10.1016/S0896-6273(00)80734-5

Keliris, G. A., Logothetis, N. K., and Tolias, A. S. (2010). The role of the primary visual cortex in perceptual suppression of salient visual stimuli. *J. Neurosci.* 30, 12353–12365. doi: 10.1523/JNEUROSCI.0677-10.2010

Koch, C., and Tsuchiya, N. (2007). Attention and consciousness: two distinct brain processes. *Trends Cogn. Sci.* 11, 16–22. doi: 10.1016/j.tics.2006.10.012

Kouider, S., and Dehaene, S. (2007). Levels of processing during non-conscious perception: a critical review of visual masking. *Philos. Trans. R. Soc. Lond. B* 362, 857–875. doi: 10.1098/rstb.2007.2093

Kovacs, I., Papathomas, T. V., Yang, M., and Feher, A. (1996). When the brain changes its mind: interocular grouping during binocular rivalry. *Proc. Natl. Acad. Sci. U.S.A.* 93, 15508–15511. doi: 10.1073/pnas.93.26.15508

Kunimoto, C., Miller, J., and Pashler, H. (2001). Confidence and accuracy of near-threshold discrimination responses. *Conscious. Cogn.* 10, 294–340. doi: 10.1006/ccog.2000.0494

Lamme, V. A. (2003). Why visual attention and awareness are different. *Trends Cogn. Sci.* 7, 12–18. doi: 10.1016/S1364-6613(02)00013-X

Lau, H. C., and Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 18763–18768. doi: 10.1073/pnas.0607716103

LeDoux, J. E. (2000). Emotion circuits in the brain. *Annu. Rev. Neurosci.* 23, 155–184. doi: 10.1146/annurev.neuro.23.1.155

Lee, S. H., Blake, R., and Heeger, D. J. (2005). Traveling waves of activity in primary visual cortex during binocular rivalry. *Nat. Neurosci.* 8, 22–23. doi: 10.1038/nn1365

Leopold, D. A., and Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature* 379, 549–553. doi: 10.1038/379549a0

Lerner, Y., Hendler, T., and Malach, R. (2002). Object-completion effects in the human lateral occipital complex. *Cereb. Cortex* 12, 163–177. doi: 10.1093/cercor/12.2.163

Logothetis, N. K., Leopold, D. A., and Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature* 380, 621–624. doi: 10.1038/380621a0

Ludwig, K., Sterzer, P., Kathmann, N., Franz, V., and Hesselmann, G. (2013). Learning to detect but not to grasp suppressed visual stimuli. *Neuropsychologia* 51, 2930–2938. doi: 10.1016/j.neuropsychologia.2013.09.035

Macmillan, N. A., and Creelman, C. D. (1991). *Detection Theory: A User's Guide.* Cambridge: Cambridge University Press.

Maier, A., Wilke, M., Aura, C., Zhu, C., Ye, F. Q., and Leopold, D. A. (2008). Divergence of fMRI and neural signals in V1 during perceptual suppression in the awake monkey. *Nat. Neurosci.* 11, 1193–1200. doi: 10.1038/nn.2173

Malach, R. (2008). The measurement problem in consciousness research. *Behav. Brain Sci.* 30, 516–517.

Martinez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., et al. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nat. Neurosci.* 2, 364–369. doi: 10.1038/7274

Meeres, S. L., and Graves, R. E. (1990). Localization of unseen visual stimuli by humans with normal vision. *Neuropsychologia* 28, 1231–1237. doi: 10.1016/0028-3932(90)90039-Q

Merikle, P. M., and Daneman, M. (2000). "Conscious vs. unconscious perception," in *The new Cognitive Neurosciences*, 2nd Edn, ed. M. S. Gazzaniga (Cambridge, MA: MIT Press), 1295–1303.

Merikle, P. M., and Reingold, E. M. (1998). On demonstrating unconscious perception: comment on Draine and Greenwald. *J. Exp. Psychol. Gen.* 127, 304–310. doi: 10.1037/0096-3445.127.3.304

Milner, A. D., and Goodale, M. A. (1995). *The Visual Brain in Action.* Oxford: Oxford University press.

Milner, A. D., and Goodale, M. A. (2006). *The Visual Brain in Action.* Oxford: Oxford University press. doi: 10.1093/acprof:oso/9780198524724.001.0001

Moradi, F., Koch, C., and Shimojo, S. (2005). Face adaptation depends on seeing the face. *Neuron* 45, 169–175. doi: 10.1016/j.neuron.2004.12.018

Naber, M., Frässle, S., and Einhäuser, W. (2011). Perceptual rivalry: reflexes reveal the gradual nature of visual awareness. *PLoS ONE* 6:e20910. doi: 10.1371/journal.pone.0020910

Norman, K. A., Polyn, S. M., Detre, G. J., and Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends Cogn. Sci.* 10, 424–430. doi: 10.1016/j.tics.2006.07.005

Overgaard, M. (2006). Introspection in science. *Conscious. Cogn.* 15, 629–633. doi: 10.1016/j.concog.2006.10.004

Overgaard, M., Lindelov, J., Svejstrup, S., Dossing, M., Hvid, T., Kauffmann, O., et al. (2013). Is conscious stimulus identification dependent on knowledge of the perceptual modality? Testing the "source misidentification hypothesis." *Front. Psychol.* 4:116. doi: 10.3389/fpsyg.2013.00116

Pasley, B. N., Mayes, L. C., and Schultz, R. T. (2004). Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron* 42, 163–172. doi: 10.1016/S0896-6273(04)00155-2

Persaud, N., Mcleod, P., and Cowey, A. (2007). Post-decision wagering objectively measures awareness. *Nat. Neurosci.* 10, 257–261. doi: 10.1038/nn1840

Pessoa, L. (2005). To what extent are emotional visual stimuli processed without attention and awareness? *Curr. Opin. Neurobiol.* 15, 188–196. doi: 10.1016/j.conb.2005.03.002

Pessoa, L., and Adolphs, R. (2010). Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nat. Rev. Neurosci.* 11, 773–783. doi: 10.1038/nrn2920

Polonsky, A., Blake, R., Braun, J., and Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nat. Neurosci.* 3, 1153–1159. doi: 10.1038/80676

Ramsoy, T. Z., and Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenol. Cogn. Sci.* 3, 1–23. doi: 10.1023/B:PHEN.0000041900.30172.e8

Rees, G. (2007). Neural correlates of the contents of visual awareness in humans. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 362, 877–886. doi: 10.1098/rstb.2007.2094

Reingold, E. M., and Merikle, P. M. (1990). On the inter-relatedness of theory and measurement in the study of unconscious processes. *Mind Lang.* 5, 9–28. doi: 10.1111/j.1468-0017.1990.tb00150.x

Roseboom, W., and Arnold, D. H. (2011). Learning to reach for 'invisible' visual input. *Curr. Biol.* 21, R493–R494. doi: 10.1016/j.cub.2011.05.036

Rothkirch, M., Stein, T., Sekutowicz, M., and Sterzer, P. (2012). A direct oculomotor correlate of unconscious visual processing. *Curr. Biol.* 22, R514–R515. doi: 10.1016/j.cub.2012.04.046

Rouder, J. N., Morey, R. D., Speckman, P. L., and Pratte, M. S. (2007). Detecting chance: a solution to the null sensitivity problem in subliminal priming. *Psychon. Bull. Rev.* 14, 597–605. doi: 10.3758/BF03196808

Sandberg, K., Timmermans, B., Overgaard, M., and Cleeremans, A. (2010). Measuring consciousness: is one measure better than the other? *Conscious. Cogn.* 19, 1069–1078. doi: 10.1016/j.concog.2009.12.013

Schmidt, T., and Vorberg, D. (2006). Criteria for unconscious cognition: three types of dissociation. *Percept. Psychophys.* 68, 489–504. doi: 10.3758/BF03193692

Schurger, A., and Sher, S. (2008). Awareness, loss aversion, and post-decision wagering. *Trends Cogn. Sci.* 12, 209–210. doi: 10.1016/j.tics.2008.02.012

Schwiedrzik, C. M., Singer, W., and Melloni, L. (2011). Subjective and objective learning effects dissociate in space and in time. *Proc. Natl. Acad. Sci. U.S.A.* 108, 4506–4511. doi: 10.1073/pnas.1009147108

Sergent, C., and Dehaene, S. (2004). Is consciousness a gradual phenomenon? Evidence for an all-or-none bifurcation during the attentional blink. *Psychol. Sci.* 15, 720–728. doi: 10.1111/j.0956-7976.2004.00748.x

Seth, A., Dienes, Z., Cleeremans, A., Overgaard, M., and Pessoa, L. (2008). Measuring consciousness: relating behavioral and neurophysiological approaches. *Trends Cogn. Sci.* 12, 314–321. doi: 10.1016/j.tics.2008.04.008

Shimaoka, D., and Kaneko, K. (2011). Dynamical systems modeling of continuous flash suppression. *Vision Res.* 51, 521–528. doi: 10.1016/j.visres.2011.01.009

Spering, M., and Carrasco, M. (2012). Similar effects of feature-based attention on motion perception and pursuit eye movements at different levels of awareness. *J. Neurosci.* 32, 7594–7601. doi: 10.1523/JNEUROSCI.0355-12.2012

Spering, M., Pomplun, M., and Carrasco, M. (2011). Tracking without perceiving: a dissociation between eye movements and motion perception. *Psychol. Sci.* 22, 216–225. doi: 10.1177/0956797610394659

Snodgrass, M. (2004). The dissociation paradigm and its discontents: how can unconscious perception or memory be inferred? *Conscious. Cogn.* 13, 107–116. doi: 10.1016/j.concog.2003.11.001

Stein, T., and Sterzer, P. (2014). Unconscious processing under interocular suppression: Getting the right measure. *Front. Psychol.* 5:387. doi: 10.3389/fpsyg.2014.00387

Stein, T., Hebart, M. N., and Sterzer, P. (2011a). Breaking continuous flash suppression: a new measure of unconscious processing during interocular suppression? *Front. Hum. Neurosci.* 5:167. doi: 10.3389/fnhum.2011.00167

Stein, T., Senju, A., Peelen, M. V., and Sterzer, P. (2011b). Eye contact facilitates awareness of faces during interocular suppression. *Cognition* 119, 307–311. doi: 10.1016/j.cognition.2011.01.008

Stein, T., Peelen, M. V., and Sterzer, P. (2012). Eye gaze adaptation under interocular suppression. *J. Vis.* 12, 1. doi: 10.1167/12.7.1

Stein, T., Seymour, K., Hebart, M. N., and Sterzer, P. (2014). Rapid fear detection relies on high spatial frequencies. *Psychol. Sci.* 25, 566–574. doi: 10.1177/0956797613512509

Stein, T., and Sterzer, P. (2011). High-level face shape adaptation depends on visual awareness: evidence from continuous flash suppression. *J. Vis.* 11, 5. doi: 10.1167/11.8.5

Sterzer, P., Haynes, J. D., and Rees, G. (2008). Fine-scale activity patterns in high-level visual areas encode the category of invisible objects. *J. Vis.* 8, 1–12. doi: 10.1167/8.15.10

Sterzer, P., Jalkanen, L., and Rees, G. (2009a). Electromagnetic responses to invisible face stimuli during binocular suppression. *Neuroimage* 46, 803–808. doi: 10.1016/j.neuroimage.2009.02.046

Sterzer, P., Kleinschmidt, A., and Rees, G. (2009b). The neural bases of multistable perception. *Trends Cogn. Sci.* 13, 310–318. doi: 10.1016/j.tics.2009.04.006

Stoerig, P. (2006). Blindsight, conscious vision, and the role of primary visual cortex. *Prog. Brain Res.* 155, 217–234. doi: 10.1016/S0079-6123(06)55012-5

Szczepanowski, R., and Pessoa, L. (2007). Fear perception: can objective and subjective awareness measures be dissociated? *J. Vis.* 7, 10. doi: 10.1167/7.4.10

Szczepanowski, R., Traczyk, J., Wierzchon, M., and Cleeremans, A. (2013). The perception of visual emotion: comparing different measures of awareness. *Conscious. Cogn.* 22, 212–220. doi: 10.1016/j.concog.2012.12.003

Tong, F., and Engel, S. A. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature* 411, 195–199. doi: 10.1038/35075583

Tong, F., Meng, M., and Blake, R. (2006). Neural bases of binocular rivalry. *Trends Cogn. Sci.* 10, 502–511. doi: 10.1016/j.tics.2006.09.003

Tong, F., Nakayama, K., Vaughan, J. T., and Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron* 21, 753–759. doi: 10.1016/S0896-6273(00)80592-9

Troiani, V., Price, E. T., and Schultz, R. T. (2012). Unseen fearful faces promote amygdala guidance of attention. *Soc. Cogn. Affect. Neurosci.* 9, 133–1340. doi: 10.1093/scan/nss116

Troiani, V., and Schultz, R. T. (2013). Amygdala, pulvinar, and inferior parietal cortex contribute to early processing of faces without awareness. *Front. Hum. Neurosci.* 7:241. doi: 10.3389/fnhum.2013.00241

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Tsuchiya, N., Koch, C., Gilroy, L. A., and Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *J. Vis.* 6, 1068–1078. doi: 10.1167/w6.10.6

van Boxtel, J. J., Tsuchiya, N., and Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. *Proc. Natl. Acad. Sci. U.S.A.* 107, 8883–8888. doi: 10.1073/pnas.0913292107

Vizueta, N., Patrick, C. J., Jiang, Y., Thomas, K. M., and He, S. (2012). Dispositional fear, negative affectivity, and neuroimaging response to visually suppressed emotional faces. *Neuroimage* 59, 761–771. doi: 10.1016/j.neuroimage.2011.w07.015

Vuilleumier, P. (2005). How brains beware: neural mechanisms of emotional attention. *Trends Cogn. Sci.* 9, 585–594. doi: 10.1016/j.tics.2005.10.011

Watanabe, M., Cheng, K., Murayama, Y., Ueno, K., Asamizuya, T., Tanaka, K., et al. (2011). Attention but not awareness modulates the BOLD signal in the human V1 during binocular suppression. *Science* 334, 829–831. doi: 10.1126/science.1203161

Wilke, M., Logothetis, N. K., and Leopold, D. A. (2006). Local field potential reflects perceptual suppression in monkey visual cortex. *Proc. Natl. Acad. Sci. U.S.A.* 103, 17507–17512. doi: 10.1073/pnas.0604673103

Willenbockel, V., Lepore, F., Nguyen, D. K., Bouthillier, A., and Gosselin, F. (2012). Spatial frequency tuning during the conscious and non-conscious perception of emotional facial expressions – an intracranial ERP study. *Front. Psychol.* 3:237. doi: 10.3389/fpsyg.2012.00237

Williams, M. A., Morris, A. P., Mcglone, F., Abbott, D. F., and Mattingley, J. B. (2004). Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *J. Neurosci.* 24, 2898–2904. doi: 10.1523/JNEUROSCI.4977-03.2004

Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Res.* 24, 471–478. doi: 10.1016/0042-6989(84)90044-0

Wunderlich, K., Schneider, K. A., and Kastner, S. (2005). Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nat. Neurosci.* 8, 1595–1602. doi: 10.1038/nn1554

Xu, S., Zhang, S., and Geng, H. (2011). Gaze-induced joint attention persists under high perceptual load and does not depend on awareness. *Vision Res.* 51, 2048–2056. doi: 10.1016/j.visres.2011.07.023

Yamashiro, H., Yamamoto, H., Mano, H., Umeda, M., Higuchi, T., and Saiki, J. (2013). Activity in early visual areas predicts interindividual differences in binocular rivalry dynamics. *J. Neurophysiol.* 111, 1190–1202. doi: 10.1152/jn.00509.2013

Yang, E., and Blake, R. (2012). Deconstructing continuous flash suppression. *J. Vis.* 12, 8. doi: 10.1167/12.3.8

Yokoyama, T., Noguchi, Y., and Kita, S. (2013). Unconscious processing of direct gaze: evidence from an ERP study. *Neuropsychologia* 51, 1161–1168. doi: 10.1016/j.neuropsychologia.2013.04.002

Yuval-Greenberg, S., and Heeger, D. J. (2013). Continuous flash suppression modulates cortical activity in early visual cortex. *J. Neurosci.* 33, 9635–9643. doi: 10.1523/JNEUROSCI.4612-12.2013

Zadbood, A., Lee, S. H., and Blake, R. (2011). Stimulus fractionation by interocular suppression. *Front. Hum. Neurosci.* 5:135. doi: 10.3389/fnhum.2011.w00135

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 06 March 2014; paper pending published: 01 April 2014; accepted: 28 April 2014; published online: 19 May 2014.

Citation: Sterzer P, Stein T, Ludwig K, Rothkirch M and Hesselmann G (2014) Neural processing of visual information under interocular suppression: a critical review. Front. Psychol. ***5****:453. doi: 10.3389/fpsyg.2014.00453*

This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

REVIEW ARTICLE
published: 27 May 2014
doi: 10.3389/fpsyg.2014.00475

Sustained invisibility through crowding and continuous flash suppression: a comparative review

***Nathan Faivre*[1,2] *, *Vincent Berthet*[3] *and Sid Kouider*[4]**

[1] Division of Biology, Computation and Neural Systems, California Institute of Technology, Pasadena, CA, USA
[2] Laboratory of Cognitive Neuroscience, Brain Mind Institute, School of Life Sciences, École Polytechnique Fédérale de Lausanne, Lausanne, Switzerland
[3] University of Lorraine, InterPsy, Nancy, France
[4] Laboratoire de Sciences Cognitives et Psycholinguistique, EHESS/CNRS/ENS-DEC, Paris, France

Edited by:
Julien Dubois, California Institute of Technology, USA

Reviewed by:
Ramakrishna Chakravarthi, University of Aberdeen, UK
Guido Hesselmann, Charité Campus Mitte, Germany

****Correspondence:***
Nathan Faivre, Laboratory of Cognitive Neuroscience, Brain Mind Institute, School of Life Sciences, École Polytechnique Fédérale de Lausanne, AI 2201.2 (Bâtiment AI), Station 19, CH-1015 Lausanne, Switzerland
e-mail: nathan.faivre@epfl.ch

The study of non-conscious vision benefits from several alternative methods that allow the suppression of an image from awareness. Here, we present and compare two of them that are particularly well-suited for creating sustained periods of invisibility, namely visual crowding and continuous flash suppression (CFS). In visual crowding, a peripheral image surrounded by similar flankers becomes impossible to discriminate. In CFS, an image presented to one eye becomes impossible to detect when rapidly changing patterns are presented to the other eye. After discussing the experimental specificities of each method, we give a comparative overview of the main empirical results derived from them, from the mere analysis of low-level features to the extraction of semantic contents. We conclude by proposing practical guidelines and future directions to obtain more quantitative and systematic measures of non-conscious processes under prolonged stimulation.

Keywords: visual crowding, continuous flash suppression, unconscious processing, awareness, consciousness

INTRODUCTION

For long, the most prevalent method used to disrupt visual awareness was masking, which consists in presenting a stimulus very briefly, in temporal contiguity with noise patterns (Breitmeyer and Ogmen, 2006). Visual masking has been extremely fruitful in describing both the architecture of the visual system and the properties of non-conscious vision (Kouider and Dehaene, 2007). Yet, as masked stimuli become visible when presented for longer than a few 10s of milliseconds, masking is not well suited for the investigation of cognitive functions requiring sustained stimulation such as motion processing, perceptual learning, sequential learning, visual search, temporal integration, etc.

In this review, we present and compare two techniques that, contrary to masking, allow for prolonged stimulation while maintaining a reliable control of awareness. The first method, visual crowding, makes a peripheral object surrounded by similar flankers impossible to discriminate, so that one cannot determine consciously some of its specific features like its angular orientation, shape, or color (Levi, 2008; Pelli and Tillman, 2008; Whitney and Levi, 2011). The second method, continuous flash suppression (CFS), renders an object presented to one eye undetectable when the other eye is flashed with a stream of rapidly changing patterns, so that one cannot determine consciously whether the stimulus is present or absent (Tsuchiya and Koch, 2005; for reviews see Lin and He, 2009; Sterzer et al., 2014). A major distinction between crowding and CFS is at the phenomenological level: while crowding prevents stimulus discriminability, CFS prevents stimulus detectability (although situations of partial awareness exist in CFS, see below). Hereafter, unless specified, "invisibility" refers to the absence of discrimination under crowding (i.e., one feature of interest is not consciously perceived, although the presence vs. absence of the stimulus is detected), and to the absence of detection under CFS (i.e., the presence vs. absence of one feature of interest or the whole stimulus is not detected). We focused on CFS and crowding as they constitute, as of today, the two most suited methods to study the temporal dynamics of conscious vs. non-conscious vision. Although other methods can induce long periods of invisibility, they are not suited for psychophysical procedures (e.g., inattentional blindness, which is effective for a few trials only), and they do not allow for a strict control of stimulus duration (e.g., binocular rivalry or bistable figures, in which visibility fluctuates erratically over time; see Kim and Blake, 2005 for a review). The phenomena of crowding and CFS are driven by specific properties of the visual system and constitute by themselves specific research questions. Only those that are relevant for the field of non-conscious vision will be covered here, as our primary goal is to offer a description of how these two methods contribute to the study of non-conscious perception, and by extension to our understanding of the mechanisms underlying consciousness. After discussing the specificities implied by both methods in terms of experimental design and procedure, we give a comparative overview of the main empirical results derived from each of them. In light of this reviewing work, we propose criteria for choosing one method over the other depending on the research question at hand. In addition, we diagnose three kinds of methodological limitations commonly found in empirical studies: the use of "all-or-none" experimental designs, the absence of methodological comparisons, and the lack of systematicity when estimating stimulus visibility. Accordingly, we propose tentative guidelines to overcome those limitations and to evaluate, in a more quantitative and systematic fashion, the nature of non-conscious vision.

HOW CFS AND CROWDING ARE USED?

CFS and crowding are of great relevance to study non-conscious processes involving long-lasting stimuli. Although both methods can be used alternatively in this context, they are supported by different mechanisms, and are associated with distinct subjective experiences (see **Figure 1**). Contrary to crowding which is a natural phenomenon occurring during normal vision, CFS has been developed explicitly as a tool to study non-conscious processes. Therefore, the psychophysical properties of CFS are far less described than those of crowding. Hence, the following description is based on both published results and personal, undocumented observations which we hope summarize the general opinion of researchers in the field.

HOW TO ARRANGE STIMULI?

As mentioned above, in CFS, the stimulus of interest is typically presented foveally and in isolation to the non-dominant eye, while the dominant eye is flashed with a series of salient patterns called mondrians and changing every 100 ms. In order for suppression to be reliable, the mondrians have to share a maximum of featural similarities with the stimulus of interest, notably in terms of shape, spatial frequency, or color (Hong and Blake, 2009; Zadbood et al., 2011; Yang and Blake, 2012). Crowding involves the binocular presentation of a peripheral stimulus surrounded by similar flankers. Importantly, crowding does not depend on stimulus size (Tripathy and Cavanagh, 2002), which allows for preventing awareness of relatively large stimuli (i.e., around 5° of visual angle; to our knowledge, no study has systematically investigated this aspect with CFS). Typically, the eccentricity between the center of the stimulus of interest and gaze location ranges from 5 to 20° of visual angle. According to an empirical law, the center-to-center spacing between the stimulus of interest and its flankers must be inferior to half the eccentricity in order for crowding to occur (Bouma, 1970). In addition, the degree of eccentricity and critical spacing needed to induce crowding varies depending on several factors such as the stimulus complexity (e.g., number and density of features, see Bernard and Chung, 2011), and the similarity between the stimulus of interest and its flankers (e.g., in terms of shape, see Kooi et al., 1994, or spatial frequency, see Chung et al., 2001), as well as their spatial arrangement (Livne and Sagi, 2007, 2010; Saarela et al., 2009; Manassi et al., 2012). Even though crowding applies to simple stimuli (van den Berg et al., 2007), one can notice that the level of crowding necessary to reach chance-level discrimination is usually obtained at smaller eccentricities for multi-feature symbols (e.g., typically 5° for Chinese pictographs, see Yeh et al., 2012) than for single feature stimuli (e.g., typically 20° for oriented lines, see Faivre and Kouider, 2011a)[1]. Accordingly, the disruption of awareness for such simple stimuli might involve not only crowding, but also unspecific mechanisms leading to signal loss at high eccentricities in the visual field (e.g., decrease of attentional amplification, decrease of photo-receptors

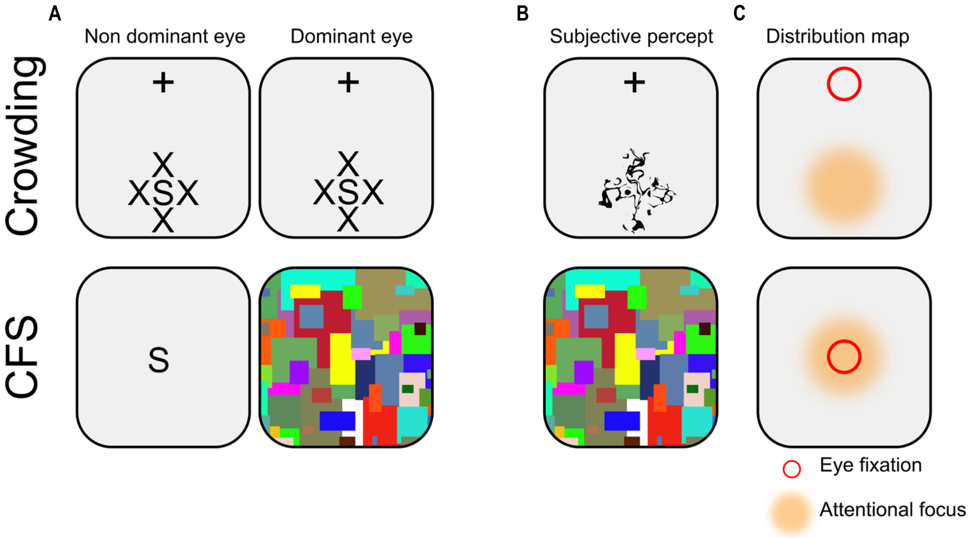


FIGURE 1 | Illustration of typical crowding and CFS displays. **(A)** Schematic representation. In crowding, participants stare at a fixation cross (which here appears at the top of the screen), while a stimulus of interest (here the letter S) is presented in the periphery of the visual field, surrounded by similar flankers (here, the letters X). Note that the display is constant across eyes. In CFS, the stimulus of interest is usually presented foveally to the non-dominant eye, while the dominant eye receives a stream of rapidly changing pattern called mondrians. **(B)** Subjective percept. In crowding, observers report seeing a jumbled array of letters in the periphery (i.e., discrimination, but not detection is impeded). In CFS, observers typically report seeing only the mondrians (i.e., both discrimination and detection are impeded). **(C)** Distribution map. In crowding, eye fixation (depicted here by a red square) and attentional focus (depicted here by an orange area) are always dissociated (i.e., endogenous attention), while they are usually conjoint in CFS.

---

[1] Discrimination with ~75% accuracy was obtained at low eccentricities for single features like orientation (2.5° in Parkes et al., 2001), size, saturation, and hue (2–15° in van den Berg et al., 2007). Further research is needed in order to establish whether crowding differs between single and multi-feature stimuli.

in the peripheral retina, poor sensitivity in the high frequency domain etc.). Note however, that such peripheral limitations can be counter-balanced by scaling up stimuli, as the extent of crowding does not scale with stimulus size (Tripathy and Cavanagh, 2002). As opposed to crowding, the efficacy of CFS does not seem to correlate with stimulus complexity, which may qualify the latter as a preferred method for preventing awareness of simple, single feature stimuli like oriented lines, or color patches.

HOW LONG CAN WE KEEP IT INVISIBLE?

The duration of stimulation is a determinant factor in experimental designs for two main reasons. First, long-lasting stimulation allows for studying the non-conscious processing of dynamic stimuli (e.g., motion, see below for empirical results). Second, it allows for manipulating stimulus onset asynchronies (SOA) independently of visibility, contrary to what happens during backward masking in which an increase of SOA is usually associated with an increase in visibility (Weisstein and Haber, 1965). Note that longer is not necessarily better, as increasing stimulus duration can have the consequence of inversing facilitatory priming effects into inhibitory habituation effects for stimuli rendered invisible, whether it is for crowding (Faivre and Kouider, 2011a) or for CFS (Barbot and Kouider, 2012; Faivre and Koch, 2014a).

How sustained is invisibility under crowding and CFS? Although no study investigated directly whether peripheral stimuli could escape crowding after relatively long exposures (i.e., minutes), previous studies suggest that there is no upper limit (e.g., Kooi et al., 1994). Thus, in principle, one might be able to prevent awareness for extended durations, as long as observers do not stare directly at the stimulus. This last aspect requires oculometric control, and notably the use of a gaze-contingent display, in which the stimulus of interest is replaced by a non-informative pattern as soon as the observer stops staring at the fixation cross. We called the experimental procedure fulfilling this condition gaze contingent crowding (GCC; Faivre and Kouider, 2011b; Kouider et al., 2011). Compared to crowding, oculometric control in CFS is far less developed, mostly due to the use of stereoscopes that are usually not compatible with eye-tracking (but see Rothkirch et al., 2012, for oculomotor correlates of non-conscious processing under CFS). No study investigated systematically the maximal duration of invisibility allowed by CFS. In their seminal study, Tsuchiya and Koch (2005) noted that in around 15% of trials "no part of the gray image was seen at all for the full 3-min trial." In general though, stimuli are known to break suppression after several seconds of display. In fact, the time taken by a stimulus to break suppression is now commonly used as a dependent variable for inferring non-conscious processing [i.e., "breaking CFS," see Jiang et al., 2007; and the review by Gayet et al. (2014) and Stein and Sterzer (2014) in the present volume].

HOW IMPORTANT IS ATTENTION?

Although the links between attention and consciousness are intricate and complex (Lamme, 2003; Koch and Tsuchiya, 2007; Cohen et al., 2012), there is now a general consensus that both conscious and non-conscious processes are themselves influenced by attentional mechanisms. For our purpose here, attention seems to plays a dual role. First, attentional amplification is known to decrease the impact of crowding and thus to increase visibility (Yeshurun and Rashal, 2010; to our knowledge no direct investigation of the links between attention and the strength of suppression under CFS has been performed). In addition, even without awareness, non-conscious effects are of bigger amplitude when stimuli are attended vs. unattended, both in crowding (Montaser-Kouhsari and Rajimehr, 2005; Faivre and Kouider, 2011b) and in CFS (Kanai et al., 2006; Bahrami et al., 2008; Kaunitz et al., 2011; see also the Frontiers research topic dedicated to this issue by Tsuchiya and van Boxtel, 2013). In CFS, the location of attentional focus is usually superimposed to the location of eye fixation (but see Bahrami et al., 2007; Hesselmann and Malach, 2011; Yuval-Greenberg and Heeger, 2013 for notable exceptions). By contrast, in crowding, the location of attentional focus is never superimposed to the location of eye fixation (e.g., observers stare at a fixation point presented at the top the screen, while endogenously attending to a stimulus presented at the bottom of the screen). Thus, in order to maximize effects amplitudes, participants have to deploy their attentional focus away from where they are staring at.

CAN WE CONTRAST VISIBLE AND INVISIBLE SITUATIONS AT CONSTANT STIMULATION?

One crucial condition to isolate the neural correlates of visual consciousness with a contrastive approach is to compare two states of consciousness while the stimulation remains constant (Baars, 1998). When this condition is fulfilled, observed differences between the two states of consciousness can hardly be argued to reflect confounds in terms of signal strength. This condition is well verified with ambiguous figures, binocular rivalry, or attentional blink (see Kim and Blake, 2005 for a review). Some efforts have been made to apply the same logic to visual masking: by reversing the order of masks and blanks, a stimulus is either visible when directly surrounded by blanks, or invisible when surrounded by masks (e.g., Dehaene et al., 2001). Although this method provided valuable results, one can still deplore that it only fulfills the criterion of constant stimulation at a global scale (i.e., when integrating the signal over the whole trial duration), but not at a local scale (i.e., the immediate context in which the stimulus is presented changes between conditions). In crowding, one usually contrasts visible and invisible conditions by manipulating the spacing or the similarity between the stimulus of interest and its flankers. This manipulation does not fulfill the criterion of constant stimulation, and therefore is not optimal in the context of a contrastive study of consciousness. However, by relying on psychophysical thresholding methods, it was shown that one can obtain conditions in which a crowded feature (i.e., the tilt of an oriented line) can be discriminated in some trials, but not in others, while the whole display remains constant (Faivre and Kouider, 2011a). Future studies are needed to assess whether such conditions can be obtained for multi-feature stimuli (e.g., faces).

As we mentioned above, "breaking CFS" is a popular variant of classical measures of after-effects (AE) which consists in measuring the time it takes for a stimulus to emerge into awareness despite suppression, and comparing possible differences between experimental conditions (Gayet et al., 2014; Jiang et al., 2007). Although this approach might potentially satisfy the criterion of constant stimulation, it suffers from methodological flaws, which are described in this volume [see the review by Stein and Sterzer (2014) and Gayet et al. (2014) in this research topic, as well as Stein et al., 2011]. Other studies have attempted to minimize the difference in terms of stimulation between conscious and non-conscious conditions, notably by presenting to the same eye the stimulus of interest superimposed to the mondrians in the conscious condition (e.g., Harris et al., 2011). It appears that reaching reliable perceptual changes at constant stimulation still requires efforts, both for crowding and CFS. Only then those two methods could be used for a strict contrastive description of the neural correlates of consciousness.

IS IT REALLY INVISIBLE?

Crowding-induced undiscriminability and CFS-induced undetectability represent two qualitatively distinct perceptual impairments. It implies that crowding and CFS stem from different mechanisms that may be responsible for some of the specific features we describe hereafter. Although the extent of crowding varies depending on stimuli and participants, it is rather stable over time, which insures the possibility of prolonged experimental sessions and therefore accurate measures (but see Chung, 2007; Sun et al., 2010; Hussain et al., 2012 for learning effects during crowding occurring across daily experimental sessions). In CFS, a decrease of contrast detection thresholds after extensive training was recently documented (Ludwig et al., 2013). In addition, we noticed that a small proportion of observers (∼5%) remain partially or completely immune to CFS: in some cases, binocular fusion seems absent, so that the stimulus of interest appears superimposed to the mondrians. In some other cases, suppression appears to break after shorter and shorter durations over an experimental session, which undermines the possibility of displaying long-lasting stimuli without awareness (this applies specifically to dynamic stimuli, see below). These observations are mainly based on personal experience, and inter-individual differences remain to be tested systematically for both methods. Likewise, no study has directly compared the causes of discrimination vs. detection impairments occurring respectively in crowding and CFS.

HOW ECOLOGICAL IS IT?

As any sensory organs, the visual system is tuned according to the optical properties naturally present in the environment. Therefore, the contrast between conscious and non-conscious vision may be most accurate when performed in ecological conditions, which mimic the natural environment. As noted above, crowding is a natural phenomenon, occurring when exploring any visual scene composed of multiple objects appearing in the periphery of the visual field. By contrast, one rarely faces two rival stimuli presented to each eye, one of them being much more salient than the other as it is the case in CFS. In the next section, we will assess whether the apparent ecological superiority of crowding over CFS is reflected in terms of empirical results.

LEVELS OF REPRESENTATION FOR NON-CONSCIOUS CONTENTS

In this part, we present the main findings obtained for stimuli rendered invisible with CFS and crowding, at different levels of visual processing: single features, motion signals, multi-feature objects (including faces), and semantic contents. By features, we mean discrete components of an image that are detected independently of each other (Suchow and Pelli, 2013). By semantic content, we refer to the meaning conveyed by a physical signal. We only review results that are based on indirect measures of non-conscious processing, whereby a modulation of neural or behavioral responsiveness follows the presentation of an invisible stimulus. Hence, we do not cover the literature based on the "breaking CFS" technique, whose potential confounds in terms of partial awareness are discussed in this research topic (see, Gayet et al., 2014; Stein and Sterzer, 2014).

NON-CONSCIOUS PROCESSING OF SINGLE FEATURES

Low-level after-effects

Before the emergence of CFS about a decade ago, several studies showed that simple features rendered invisible by binocular rivalry produce specific sensory illusions called AE. The observation of such AE is considered as a behavioral signature of non-conscious processing, for simple features such as tilted lines (tilt AE, Wade and Wenderoth, 1978), square-wave gratings (spatial frequency AE, Blake and Fox, 1974), McCollough-type gratings (orientation-contingent color AE, White et al., 1978), and translational motion (motion AE, Lehmkuhle and Fox, 1975; O'Shea and Crassini, 1981).

Building upon those precursors, and under more reliable suppression conditions (Tsuchiya et al., 2006), similar results were found under CFS regarding tilt AE (Bahrami et al., 2008). Likewise, crowded tilted lines are also known to induce tilt AE (He et al., 1996), and priming (Montaser-Kouhsari and Rajimehr, 2005; Faivre and Kouider, 2011a). Yet, spatial frequency and orientation-contingent color AE remain to be tested under both CFS and crowding.

Brightness is another low-level feature whose perception under CFS has been studied using contextual illusions. On the one hand, it was shown that the simultaneous brightness contrast illusion (i.e., a gray circle appearing brighter against a dark background than against a light background) persists even when the spatial context inducing the illusion (the background region that surrounded two physically identical target circles) was suppressed from awareness by CFS (Harris et al., 2011). Yet, the same study reported that the Kanizsa triangle illusion (i.e., the illusion of a luminance contour induced by spatially distinct elements prompting the visual system to assume the presence of an occluding surface) did not persist when the inducer elements were suppressed from awareness[2]. These findings suggest that under CFS, the low-level processes involved in brightness perception (e.g., background luminance) can occur without awareness, while the higher-level ones involved in the assignation of surface borders through perceptual completion do not. Interestingly, positive evidence for the Kanizsa triangle illusion was found when the inducer elements were crowded (Lau and Cheung, 2012).

Over the years, a debate has emerged as to know whether low-level AE such as the tilt AE are stronger when induced by visible compared to invisible stimuli. He et al. (1996) first suggested that crowding had no influence on the amplitude of tilt AE induced

---

[2] See Wang et al. (2012) for positive results based on bCFS.

by high-contrast gratings. On the other hand, it was shown that both tilt and motion AE were smaller when low-contrast stimuli were rendered invisible by binocular rivalry and crowding, compared to a situation of full visibility (Blake et al., 2006). This study further suggested that the independence between AE amplitudes and visibility found previously might stem from a saturation of the adaptive response at high stimulus contrast. Yet, a subsequent study showed that when manipulating carefully attentional amplification, low-contrast stimuli could induce the same AE whether crowded or not (Bi et al., 2009). Finally, evidence from fMRI indicated that crowding had a detrimental effect on AE amplitude at the level of V2/V3, but not at the level of V1 (where tilt AE are supposed to stem from, see Fang and He, 2008). Taken together, these results suggest that crowding may be seen as a bottleneck impacting visual processes differently depending on their position along the visual pathways.

If the independence between AE amplitude and crowding remains debated, the evidence is clearer for CFS: the very first paper introducing CFS showed that it had a detrimental effect on the amplitude of after-images (Tsuchiya and Koch, 2005), and recent findings using fMRI strengthened this idea by showing that CFS decreases the activity from signals as early as in the primary visual cortex (Watanabe et al., 2011; Yuval-Greenberg and Heeger, 2013). Comparing these results with those of Fang and He (2008) described above, one could deduce that crowding impacts visual processes at later stages compared to CFS. However, considering the high variability across experiments, we argue that clear conclusions should be drawn from systematic comparisons only (see discussion).

NON-CONSCIOUS PROCESSING OF MOTION SIGNALS

As we mentioned in the introduction, CFS and crowding present the advantage of maintaining stimuli out of awareness for potentially long durations. So far, most studies that took advantage of this property focused on motion processing, by measuring motion AE from invisible stimuli. In CFS, translational motion has first been shown to induce motion AE that did not transfer across eyes, suggesting that the underlying processes are quite low-level (Maruya et al., 2008). Yet, with a slightly different setup, AE induced by translational and spiral motion were found to transfer across eyes, and to depend on attentional amplification (Kaunitz et al., 2011). Recently, AE from apparent and biological motions (i.e., point-light walkers) were found under CFS (Faivre and Koch, 2014b). However, it was found that the extent of temporal integration was smaller under CFS than in condition of full visibility (i.e., ∼100 ms vs. ∼1s for apparent motion, and ∼1 vs. ∼3s for biological motion, respectively). Taken together, these results suggest that motion processing is enabled under CFS at various levels of complexity, but with restricted periods of temporal integration. Interestingly, it was also shown that the processing of implied motion (i.e., static pictures depicting someone or something moving) was not enabled in the absence of awareness, suggesting that CFS has a detrimental effect not only on temporal but also spatial integrative processes (Faivre and Koch, 2014b).

Under crowding, translational motion is known to shift the apparent location of a subsequent stimulus (Whitney, 2005; Bressler and Whitney, 2006), while spiral motion (Aghdaee, 2005; Aghdaee and Zandvakili, 2005) and apparent motion (Rajimehr et al., 2004) also induce AE. In addition, crowded biological motion in the form of dynamic facial expressions were found to be processed despite crowding, notably through the dorsal visual pathway (Faivre et al., 2012b, see below). It appears from these findings that, as in CFS, motion processing at various levels of complexity is enabled under crowding.

NON-CONSCIOUS PROCESSING OF MULTI-FEATURE OBJECTS

Face stimuli

Among all stimuli composed of multiple features, faces have undoubtedly triggered the most interest in the field of non-conscious vision, including studies relying on CFS and crowding. Beyond its obvious ecological value, a single face stimulus conveys multiple levels of information which allows for probing non-conscious processing at several levels of complexity. Here, we review the evidence for non-conscious face processing along two axes: the representation of facial identity and the emotional processing of facial expression.

Jiang and He (2006) were the first to focus on face processing under CFS with fMRI. They found that the fusiform face area was more activated by fearful or neutral faces compared to scramble faces. In addition, they found that the amygdala and superior temporal sulcus were more activated by fearful compared to neutral faces. Recently, it was found that this activation in the superior temporal sulcus was only present in participants with high negative affectivity (a dispositional trait relevant to psychopathology, see Vizueta et al., 2012). A subsequent study reported that category-specific responses induced by invisible faces vs. houses in fusiform and parahippocampal cortices can be only obtained when using multivariate pattern analysis, rather than univariate techniques, suggesting that the fine-scale pattern of activity within these areas encodes the features of invisible objects (Sterzer et al., 2008). Building upon these fMRI studies, the same research teams then focused on the electromagnetic correlates of non-conscious face processing. Jiang et al. (2009) found electroencephalographic responses to faces vs. scrambled faces in posterior occipital areas (between 140 ms and 200 ms after stimulus onset, arguably similar to the classical N170 component for face processing), followed by responses to fearful vs. neutral faces along superior temporal regions 220 ms after stimulus onset. Sterzer et al. (2009) confirmed the category-specific differences they found with fMRI in a magnetoencephalographic study, by documenting an M170 component in response to invisible faces vs. houses along the fusiform cortex. Taken together, these results based on hemodynamic and electromagnetic correlates of neural activity suggest that the signals conveying both face-specific information (i.e., face vs. scramble or fearful vs. neutral face) and category-specific information (i.e., face vs. house) are not abolished by CFS.

At the behavioral level, the evidence for processing of facial identity under CFS is less convincing. Using a method similar to CFS, Moradi et al. (2005) first attempted to measure identity AE, that is a bias for the perception of a specific facial shape after the observer is exposed to an adapting face that has opposite global features (its "antiface"). They found that such identity AE occurred when the adapting face was visible, but completely vanished when it was invisible. Later, Stein and Sterzer (2011) reported that identity AE could actually be induced by invisible faces, though with a reduced amplitude, and without interocular transfer (i.e., when the adaptation face and the target are presented to different eyes), suggesting that it probably stemmed from low-level processes. Similarly, Barbot and Kouider (2012) found that the identity of invisible faces induced repetition priming effects, but with no interocular transfer: participants were faster to categorize a target face as famous when it was preceded by an invisible identical vs. different prime face presented to the same eye. As primes and targets were of different sizes (i.e., 20% size difference), it was argued that these priming effects genuinely reflected non-conscious processing of facial identity. Yet, it was recently found that the similarity between a prime and a target differing only in terms of size could be captured as early as in the primary visual cortex, up to 70% of size difference (Faivre and Koch, 2014a). This raises the possibility that identity priming for faces reflects low-level overlap rather than the activation of face representations *per se*. In addition, the existence of identity repetition priming in conditions of complete unawareness was recently challenged by a study reporting that priming effects are indeed induced by faces whose identity is invisible, but critically, only when lower level features like color or location are visible (i.e., partial awareness, see Mudrik et al., 2013). We come back to the issue of partial awareness in the discussion. Overall, the behavioral evidence for the processing of facial identity remains inconclusive.

Now regarding emotional processing under CFS, an influential study first reported that observers' attention could be attracted to or repelled from invisible erotic stimuli, depending on observer's gender and sexual orientation (Jiang et al., 2006). Later, it was shown that invisible adaptors depicting facial expressions of anger, fearfulness and happiness could bias the way a subsequent target face was perceived (i.e., facial expression AE, see Adams et al., 2010). Contrary to what was observed for the processing of identity, these results cannot stem from low-level retinotopic similarities, as adaptor and target stimuli were presented to opposite sides of the visual field and to different eyes. These two studies reinforced the idea of a "special status" for emotional stimuli, as objects that are processed without awareness notably along subcortical routes (Tamietto and de Gelder, 2010). Yet, facial expression AE were subsequently dismissed on the basis that it probably stemmed from residual visibility and attentional confounds (Yang et al., 2010; see Adams et al., 2011 for a response). Supporting this idea, another study showed that aftereffects from gender and race information were absent under strict control of awareness (Amihai et al., 2011). New elements to this debate were recently added by two studies, in which invisible fearful faces were found to change skin-conductance responses, both in the context of fear conditioning (Raio et al., 2012) and preference judgments (Lapate et al., 2013). In addition, preference judgments biases were found to be induced by angry – but not happy – faces rendered invisible by CFS (Almeida et al., 2013, but see Faivre et al., 2012a for negative results under masking and CFS; de Zilva et al., 2013 for negative results about the mere exposure effect under CFS). We can conclude from this group of recent studies that unlike facial identity, facial expressions rendered invisible by CFS elicit responses that can be captured at the behavioral level[3].

Under crowding, Faivre and Kouider (2011b) showed repetition priming of facial identity when the prime and target were presented 15° away from each other, suggesting that unlike what was shown for CFS (Barbot and Kouider, 2012), identity processing under crowding does not depend on retinotopic similarity. Furthermore, we showed that crowded facial expressions can bias subsequent affective judgments of neutral pictographs (happy faces elicited more pleasant judgments than angry faces, see Kouider et al., 2011). Moreover, the preference bias induced by crowding faces was not only induced by static (i.e., pictures) but also by dynamic (i.e., videos) facial expressions. Using fMRI coupled with univariate analysis, it was found that compared to a neutral face, static happy faces activated primarily the ventral visual pathway including the fusiform face area, which was functionally connected to the amygdala (Faivre et al., 2012b). By contrast, dynamic happy faces triggered the dorsal visual pathway (including the posterior parietal cortex) and the substantia innominata, a structure contiguous with the dorsal amygdala. To our knowledge, no multivariate pattern analysis has been applied to try to decode the content of crowded stimuli. Along the same lines, it was shown that crowded emotional faces could influence a conscious judgment (assessing the average emotion resulting of six flanker faces and one target crowded face) while the same inverted and scrambled faces could not (Haberman and Whitney, 2007, 2009). Like our results, this finding shows that despite preventing object recognition, crowding does not impede the processing of emotional information extracted from objects.

Tool stimuli and the dorsal visual stream

Besides faces, the processing of tools under CFS has also received much attention. Using fMRI, Fang and He (2005) first revealed that suppressed pictures of tools specifically activate the dorsal visual pathway, which is thought to support the guidance of actions (Goodale and Milner, 1992). At the behavioral level, it was shown that suppressed pictures of tools – but not of non-manipulable objects like animals – could facilitate the categorization of subsequent targets (i.e., categorical priming, see Almeida et al., 2008, 2010), suggesting that non-conscious processing in the dorsal – but not ventral – visual pathway can be used for recognizing manipulable objects. Recently, this finding was challenged by a study revealing that similar priming effects could actually be induced by any kind of elongated objects, rather than specifically manipulable objects (Hebart and Hesselmann, 2012; Sakuraba et al., 2012). As the previous priming effects may stem from such low-level confounds, the level of processing undergone by invisible tool stimuli remains unclear. Relying on multivariate analysis of blood-oxygen-level dependent signal, Hesselmann and Malach (2011) showed that features from invisible tools were encoded in the lateral occipital cortex, which rules

---

[3] Interestingly, much more positive results were found using the breaking CFS method (Jiang et al., 2007; Yang et al., 2007; Tsuchiya et al., 2009; Zhou et al., 2010; Stein et al., 2012, 2013; Stewart et al., 2012; Gray et al., 2013). These results and the apparent discrepancy with the ones we reviewed are discussed in this research topic (see Gayet et al., 2014; Stein and Sterzer, 2014).

out the possibility that stimulus energy was so low that all high-level processes were abolished. Most importantly, they also found that CFS equally reduced brain activity in the ventral and dorsal visual pathways, which challenges the original claim that CFS has no or little influence on the dorsal visual pathway (Almeida et al., 2008). The claim that CFS disrupts the ventral but not the dorsal visual pathway is further debated, as one study documented the capacity to grasp visually suppressed stimuli (Roseboom and Arnold, 2011, but see Ludwig et al., 2013; see also the comment on the study by Roseboom and Arnold, 2011 from the same authors).

Regarding crowding, although several lines of evidence suggest that multi-feature objects like arrows (Faivre and Kouider, 2011b), sequences of geometric shapes (Atas et al., 2013), or naturalistic objects (Fischer and Whitney, 2011) are processed in the absence of conscious discrimination, no study has investigated directly the processing of crowded tools. Yet, it was found that crowding decreases to the same extent the spatial resolution of both visually guided reaching and perception, suggesting that it impacts both the ventral and the dorsal visual pathways (Bulakowski et al., 2009).

NON-CONSCIOUS PROCESSING AT THE SEMANTIC LEVEL

As of today, it remains unclear whether stimuli rendered invisible by CFS can be processed up to the semantic level. Combining the semantic-priming procedure with binocular rivalry, Zimba and Blake (1983) first presented prime words to an eye during either dominance or suppression phases of binocular rivalry. A semantic-priming effect (here on response times in a lexical decision task) was observed only when prime words were presented during dominance phases, suggesting that semantic processing is disabled during suppression phases.

Kang et al. (2011) extended this work by combining the semantic-priming procedure with CFS, and using the N400 component of human event-related potentials (ERPs) as an electrophysiological index of semantic processing. Here, an invisible target word (e.g., apple) was preceded by a semantically related (e.g., orange) vs. unrelated (e.g., doctor) prime word. Although target words usually elicit N400 components of smaller amplitudes when preceded by semantically related vs. unrelated primes, no such modulation was observed when the target was rendered invisible by CFS. As in binocular rivalry, this result lead the authors to conclude that semantic processing of words was disabled under CFS (but see Heyman and Moors, 2012, for possible theoretical and methodological issues).

Contradicting this negative result, it was recently shown that complex – rather than single – semantic stimuli (e.g., multiple-word phrases, basic equations) rendered invisible by CFS for longer durations (i.e., up to 2 s) can still be processed (Sklar et al., 2012). For instance, the result of an invisible equation (e.g., $9 - 3 - 4 =$) was found to facilitate the response to a subsequent target number congruent to the equation's solution. This suggests that the equation had been non-consciously solved by the time the target appeared. In line with this study, Zabelina et al. (2013) investigated the semantic processing of triplets of words under CFS. In each trial, participants had to solve a compound remote associate problem, that is finding a word (e.g., apple) common to three seemingly unrelated words that were suppressed for seconds before being fully visible (e.g., pine, crab, sauce). Participants solved word problems faster following suppressed problem words than following suppressed irrelevant words. Interestingly, this priming effect was observed only when participants reached the solution by analysis rather than by insight, which led the authors to suggest that semantic processing but not semantic integration of the word triads occurred non-consciously. Here, however, since there was no physical difference between primes and targets (i.e., the task was performed once the triplet words became visible), priming may have stemmed from a perceptual rather than semantic facilitation. Indeed, participants may have processed the triplet words at a perceptual but not semantic level, which nevertheless would facilitate responses on the triplet words when they become visible.

In the same vein, using a setting in which participants heard a verbal label before performing a simple detection task wherein stimuli were pictures of familiar objects rendered invisible by CFS, Lupyan and Ward (2013) found that valid labels (words semantically related to the object) improved performance while invalid labels decreased performance. Yet, they also reported that the effectiveness of labels varied as a function of the match between the shape of the stimulus and the shape denoted by the label, suggesting that labels facilitated the perceptual processing of the suppressed objects rather than their semantic processing[4].

Finally, two studies have investigated whether crowded stimuli can be processed at the semantic level. Yeh et al. (2012) showed that crowded single-character Chinese words were able to induce behavioral semantic-priming effects in a lexical decision task, with an effect amplitude similar to those induced by visible Chinese words. Recently, Peng et al. (2013) combined the semantic-priming paradigm with crowding while recording ERPs. As in the CFS study by Kang et al. (2011) described above, crowding was applied to target rather than prime words. Here, participants were required to judge whether the prime and target words were semantically related or not. Semantic priming was reflected both in terms of reaction times and in the amplitude of the N400 component, although effects were of smaller amplitudes for crowded compared to uncrowded targets. However, one should note that the discriminability of crowded targets was slightly above chance-level, which questions the non-conscious origin of these effects. Interestingly though, the authors report that long-lasting presentation of crowded targets is required in order to observe semantic priming, which suggests that sustained invisibility is beneficial when probing high-level processes.

SUMMARY: WHAT CAN BE SAID OVERALL?

We here summarize what emerges from the sum of empirical results describing the depth of non-conscious processing under crowding and CFS over the last decade. First, as a tool to study non-conscious vision, it appears that the use of CFS is much more widespread than that of crowding (i.e., we numbered 50 vs. 21 studies addressing directly non-conscious processing with

---

[4] As in for what we noted regarding face processing, much more evidence of semantic processing was obtained using bCFS (Jiang et al., 2007; Costello et al., 2009; Mudrik et al., 2011; Yang and Yeh, 2011; Sklar et al., 2012).

CFS vs. crowding). Overall, there is strong behavioral evidence for the processing of simple stimuli under both CFS and crowding, including luminance and contrast (CFS: Harris et al., 2011; crowding: Lau and Cheung, 2012), orientation (CFS: Bahrami et al., 2008; crowding: He et al., 1996; Faivre and Kouider, 2011b), and motion (CFS: e.g., Maruya et al., 2008; Kaunitz et al., 2011; Faivre and Koch, 2014b; crowding: e.g., Rajimehr et al., 2004; Whitney, 2005). Efforts remain to be made regarding the respective impact of crowding and CFS on the amplitude of such low-level processes (e.g., size of AE). Regarding multi-feature objects, the literature on CFS is rather controversial. As of today, no compelling behavioral evidence supports the processing of facial identity (e.g., Moradi et al., 2005; Stein and Sterzer, 2011), even though signals conveying facial identity may be detectable at the neural level, especially when using more subtle analyses such as multivariate pattern classification (Sterzer et al., 2008). By contrast, emotional stimuli like facial expressions seem to trigger both behavioral and neural responses (e.g., Adams et al., 2010). This discrepancy between the processing of facial identity and facial expressions suggests that the latter may be processed along subcortical routes that are not fully disrupted by CFS (Tamietto and de Gelder, 2010). One can conclude that behavioral measures (i.e., priming, AE) may not be suited for detecting the weak traces left by complex stimuli rendered invisible by CFS. Yet, physiological measures like skin conductance, electromagnetic or hemodynamic responses (associated with multivariate analysis) seem to indicate that CFS does not abolish the processing of complex stimuli such as faces (facial expressions, see Raio et al., 2012 or facial identity, see Sterzer et al., 2008) or tools (Hesselmann and Malach, 2011). Similarly, two studies (Sklar et al., 2012; Zabelina et al., 2013) seem to indicate that the processing of combination of words or numbers are processed up to the semantic level, although potential low-level confounds remain to be ruled out.

Compared to CFS, the literature on crowding is more limited, but also more consistent: all studies we found report positive behavioral results for the encoding of crowded multi-feature objects, including symbols, facial identity (Faivre and Kouider, 2011b), and facial expressions (Kouider et al., 2011), up to the extraction of semantic information (Yeh et al., 2012; Peng et al., 2013; although full indiscriminability of crowded stimuli is not always warranted, see above). It is unfortunate that compared to CFS, the neural basis of non-conscious processing under crowding remains largely uncovered (see Chicherov et al., 2014 for a recent study on the neural correlate of crowding).

From low-level features to semantic content, looking exclusively at the positive results we reviewed would lead to the conclusion that virtually any kind of visual process is enabled under crowding or CFS. One could derive from this observation that stimulus awareness has no functional role during visual processing (e.g., Hassin, 2013). Yet, a large portion of the results we reviewed are far from being unequivocal. Indeed, the literature on each specific topic often includes conditions of residual awareness, negative findings which are difficult to interpret, replication failures which most likely exist but remain undocumented, or inadequate conclusions due to experimental confounds (e.g., arguing for the processing of tools vs. elongated objects, or for semantic rather than perceptual processing, see above). Hence, this heterogeneous set of studies makes the whole picture of non-conscious vision under crowding and CFS difficult to interpret. Below, we discuss some potential reasons for this difficulty, and humbly propose tentative guidelines to manage this tremendously challenging task.

Is one better than the other?

Tables 1 and **2** summarize what can be said regarding the respective advantages of crowding vs. CFS. Considering the lack of systematic methodological comparison, the criteria for choosing one or the other method mostly pertain to practical considerations. As mentioned in the introduction, if one's aim is to study the processing of simple stimuli in the complete absence of awareness (e.g., an oriented line remaining undetectable), CFS would most likely do the trick. Crowding, on the other hand, is not as potent with single feature stimuli, and only impedes stimulus discrimination. Yet, if one's aim is to measure the processing of complex objects in a natural environment (e.g., under conditions of virtual reality, see

Table 1 | Summary of the comparison of crowding and CFS on different psychophysical features.

	Crowding	**Continuous flash suppression**
Stimulation	Binocular, peripheral	Monocular, foveal
Maximal duration	Unlimited?	∼30s
Visibility impairment	Discrimination	Detection
Adjustable parameters	Eccentricity, flankers, contrast	Mondrians, contrast
Subjective change at constant stimulation	Only for tilted lines	Only with bCFS
Conditions of partial awareness	Not documented	Location, form, color
Sensitivity to attentional amplification	Yes	Yes
Efficacy for dynamic stimuli	Good	Good
Efficacy for faces	Good	Good
Efficacy for single features	Poor	Good
Robustness across subjects	Good	Fair
Compatibility with physiological measures	Good	Good

Table 2 | Summary of the comparison of crowding and CFS on the level of evidence regarding non-conscious processing of various contents.

	Crowding	Continuous flash suppression
Single features		
Tilt AE	Good, decrease of AE amplitude debated	Good, decrease of AE amplitude
Motion signals	Good	Good (decrease of temporal integration)
Faces		
Facial identity	Good	Fair (results are mixed at the behavioral level)
Facial expression	Good	Good
Tools	Lack of studies	Fair (potential low-level confounds)
Semantic	Fair (few studies, potential visibility confounds)	Fair (potential perceptual confounds)

Pizzi et al., 2012), crowding seems like a valuable alternative to CFS.

The main advantage of both crowding and CFS over the arsenal of techniques available in the field (Kim and Blake, 2005) is the possibility for sustained invisibility: a stimulus can be presented for several seconds, either in the form of a static picture or dynamic movie, while the observer accesses none or some of its features (see above). This improvement opens many research questions: how do conscious vs. non-conscious processes unfold over time? Can temporal structures spread over long durations be integrated into unique representations? For what kind of processing is sustained invisibility beneficial? One obvious case is the processing of dynamic stimuli (e.g., motion). Another one is the processing of long-lasting stimuli inducing neural fatigue (e.g., inducing tilt AE). Displaying static stimuli for long durations is known to potentially overstimulate the visual system, and transform facilitatory into inhibitory effects (see Faivre and Kouider, 2011a; Barbot and Kouider, 2012). Besides this phenomenon, several studies investigating high-level cognitive processes mentioned the benefit of using long-lasting static stimuli (i.e., several hundred of milliseconds up to 3 s) as it gives them the time necessary for elaborate processing. For instance Bahrami et al. (2010) had invisible gabor patches conveying numerosity information presented for durations up to 3 s. Sklar et al. (2012) had sentences and equations suppressed from awareness for up to 2 s. It would be interesting to test whether such non-conscious processes under crowding and CFS are enabled when shorter stimuli are used. In crowding, Peng et al. (2013) explicitly mentioned the presence of semantic priming when crowded words were presented for 1 s but not 350 ms. This is at odds with the numerous results showing that processing of words or digits presented for a few 10s of milliseconds are enabled despite masking (see Kouider and Dehaene, 2007 for a review). In those conditions, determining what is left to crowding and CFS compared to masking or other techniques requires systematic comparisons.

CROWDING AND CFS: WHAT'S NEXT?

Altogether, the numerous studies reviewed above provide a rather unclear and incomplete picture of the nature of non-conscious vision under crowding and CFS. This, in our opinion, is due to three main methodological limitations (see also Yang et al., current issue, for a standardized approach in CFS).

The first methodological limitation is that most studies rely on "all-or-none" designs, whereby only the presence vs. the absence of an non-conscious process is assessed. If enabled, this process typically gives rise to a measurable effect (e.g., priming, AE, changes of neural activity, etc.), while if it is disabled, a null effect is observed. Such null effects can be hardly interpretable, and are in fact rarely published, giving rise to a bias in the literature on non-conscious vision (i.e., file drawer effect, see Rosenthal, 1979). Thus, rather than "all-or-none" designs, we argue that the field would benefit from the use of parametric designs. First, parametrization can be applied to the stimulus visibility, in order to compare a process at distinct levels of awareness (e.g., with different degrees of crowding or CFS). This allows for estimating quantitatively the role of stimulus visibility for a given process in terms of effects' amplitude (e.g., the amplitude of tilt and motion AE at various levels of crowding and binocular rivalry, see Blake et al., 2006), effects' dynamics (e.g., the time it takes for an effect to arise over the experimental session) or effects' robustness (e.g., how sensitive an effect is to attentional manipulations). Secondly, parametrization can be applied to the stimulus complexity, in order to compare conscious and non-conscious processes at distinct levels of representation (e.g., probing facial identity and expression with the same stimuli). In this context, the observation of a null effect obtained at one level of representation may be confirmed by the presence of a positive effect showing that the stimulus is nevertheless processed at a lower level of representation (e.g., evidence for lexical but not semantic processing). Accordingly, one would be able to estimate the impact of crowding and CFS at distinct levels along the visual pathways for a single stimulus, as it was tentatively done in binocular rivalry (Nguyen et al., 2003). Not only this strategy would help probing the limits of non-conscious vision more systematically, but also lead to a better understanding of the mechanisms at the origin of invisibility under crowding and CFS.

The second methodological limitation is that most studies usually measure non-conscious processing relying on a single technique to prevent stimulus awareness (but see Blake et al., 2006; Almeida et al., 2008, 2013; Kanai et al., 2010; Faivre et al., 2012a; Stein et al., 2013, for examples of studies measuring a process under different techniques). Considering that each study uses different experimental setups (i.e., in terms of stimulus set, hardware, indirect measure of processing, etc.), it is difficult to conclude about the superiority of one technique over the other. Yet, if one wants to describe the limits of non-conscious vision, one has to disentangle what can be attributed to the method employed to render the stimulus invisible (i.e., stimulus duration, contrast, position in the visual field, etc.) and the limits attributed to the nature of non-conscious processing *per se*. This may require performing studies at larger scales, in which the dependencies between one specific process and visual awareness are assessed with a set of complementary methods and a single stimulus set.

The third methodological limitation concerns measures of stimulus awareness. Although some efforts are made at the theoretical level to reach a consensus regarding a definition for stimulus awareness (e.g., Seth et al., 2008; Sandberg et al., 2010), most studies diverge in their use of visibility measures. Objective measures include detection tasks (i.e., determinate if the stimulus is present or not), discrimination tasks (i.e., recognize a stimulus from its scrambled version), or categorization tasks (i.e., distinguish two stimuli from different categories). Invisibility is usually taken as granted from chance-level performance in any of these measures. Yet, each of them clearly implies a different definition of invisibility. For instance, performance on a detection task in a crowding experiment would be clearly above chance, as only the discriminability of a crowded stimulus is impaired (Levi, 2008). Moreover, long periods of partial awareness are described under CFS, in which observers have access to specific features of a stimulus like its color or location, but not others like its orientation (Hong and Blake, 2009; Zadbood et al., 2011). In this situation, observers are likely to perform at chance-level in one but not the other objective visibility task. The lack of consistency in the assessment of stimulus awareness is particularly problematic considering that these situations of partial awareness are known to potentially drive supposedly non-conscious effects (Kouider and Dupoux, 2004; Kouider et al., 2010; Mudrik et al., 2013). In order to refine the level of awareness associated with one or the other technique, objective measures may be used in synergy with subjective ones using either continuous (e.g., Sergent and Dehaene, 2004) or discrete scales (Ramsøy and Overgaard, 2004). Finally, each measure may be performed at the single trial level, in order to account for training or fatigue effects[5]. This is particularly relevant in case stimuli are presented for long periods of time during which awareness may fluctuate.

REFERENCES

Adams, W. J., Gray, K. L. H., Garner, M., and Graf, E. W. (2010). High-level face adaptation without awareness. *Psychol. Sci.* 21, 205–210. doi: 10.1177/0956797609359508

Adams, W. J., Gray, K. L. H., Garner, M., and Graf, E. W. (2011). On the “special” status of emotional faces... Comment on Yang, Hong, and Blake (2010). *J. Vis.* 11, 10. doi: 10.1167/11.3.10

Aghdaee, S. M. (2005). Adaptation to spiral motion in crowding condition. *Perception* 34, 155–162. doi: 10.1068/p5298

Aghdaee, S. M., and Zandvakili, A. (2005). Adaptation to spiral motion: global but not local motion detectors are modulated by attention. *Vision Res.* 45, 1099–1105. doi: 10.1016/j.visres.2004.11.012

Almeida, J., Mahon, B. Z., and Caramazza, A. (2010). The role of the dorsal visual processing stream in tool identification. *Psychol. Sci.* 21, 772–778. doi: 10.1177/0956797610371343

Almeida, J., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proc. Natl. Acad. Sci. U.S.A.* 105, 15214–15218. doi: 10.1073/pnas.0805867105

Almeida, J., Pajtas, P. E., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2013). Affect of the unconscious: visually suppressed angry faces modulate our decisions. *Cogn. Affect. Behav. Neurosci.* 13, 94–101. doi: 10.3758/s13415-012-0133-7

Amihai, I., Deouell, L., and Bentin, S. (2011). Conscious awareness is necessary for processing race and gender information from faces. *Conscious. Cogn.* 20, 269–279. doi: 10.1016/j.concog.2010.08.004

Atas, A., Faivre, N., Timmermans, B., Cleeremans, A., and Kouider, S. (2013). Nonconscious learning from crowded sequences. *Psychol. Sci.* 25, 113–119. doi: 10.1177/0956797613499591

Baars, B. J. (1998). “Contrastive phenomenology: A thoroughly empirical approach to consciousness,” in *The Nature of Consciousness: Philosophical Debates*, ed. N. J. Block (Cambridge: MIT Press), 187–201.

Bahrami, B., Carmel, D., Walsh, V., Rees, G., and Lavie, N. (2008). Unconscious orientation processing depends on perceptual load. *J. Vis.* 8, 12.1–12.10. doi: 10.1167/8.3.12

Bahrami, B., Lavie, N., and Rees, G. (2007). Attentional load modulates responses of human primary visual cortex to invisible stimuli. *Curr. Biol.* 17, 509–513. doi: 10.1016/j.cub.2007.01.070

Bahrami, B., Vetter, P., Spolaore, E., Pagano, S., Butterworth, B., and Rees, G. (2010). Unconscious numerical priming despite interocular suppression. *Psychol. Sci.* 21, 224–233. doi: 10.1177/0956797609360664

Barbot, A., and Kouider, S. (2012). Longer is not better: nonconscious overstimulation reverses priming influences under interocular suppression. *Atten. Percept. Psychophys.* 74, 174–184. doi: 10.3758/s13414-011-0226-3

Bernard, J.-B., and Chung, S. T. L. (2011). The dependence of crowding on flanker complexity and target-flanker similarity. *J. Vis.* 11, 1. doi: 10.1167/11.8.1

Bi, T., Cai, P., Zhou, T., and Fang, F. (2009). The effect of crowding on orientation-selective adaptation in human early visual cortex. *J. Vis.* 9, 13.1–13.10. doi: 10.1167/9.11.13

Blake, R., and Fox, R. (1974). Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature* 249, 488–490. doi: 10.1038/249488a0

Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., and Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 4783–4788. doi: 10.1073/pnas.0509634103

Bouma, H. (1970). Interaction effects in parafoveal letter recognition. *Nature* 226, 177–178. doi: 10.1038/226177a0

Breitmeyer, B., and Ogmen, H. (2006). *Visual Masking: Time Slices Through Conscious and Unconscious Vision*. Oxford: Oxford University Press. doi: 10.1093/acprof:oso/9780198530671.001.0001

Bressler, D. W., and Whitney, D. (2006). Second-order motion shifts perceived position. *Vision Res.* 46, 1120–1128. doi: 10.1016/j.visres.2005.10.012

Bulakowski, P. F., Post, R. B., and Whitney, D. (2009). Visuomotor crowding: the resolution of grasping in cluttered scenes. *Front. Behav. Neurosci.* 3:49. doi: 10.3389/neuro.08.049.2009

Chicherov, V., Plomp, G., and Herzog, M. H. (2014). Neural correlates of visual crowding. *Neuroimage* 93, 23–31. doi: 10.1016/j.neuroimage.2014.02.021

Chung, S. T., Levi, D. M., and Legge, G. E. (2001). Spatial-frequency and contrast properties of crowding. *Vision Res.* 41, 1833–1850. doi: 10.1016/S0042-6989(01)00071-2

Chung, S. T. L. (2007). Learning to identify crowded letters: does it improve reading speed? *Vision Res.* 47, 3150–3159. doi: 10.1016/j.visres.2007.08.017

Cohen, M. A., Cavanagh, P., Chun, M. M., and Nakayama, K. (2012). The attentional requirements of consciousness. *Trends Cogn. Sci.* 16, 411–417. doi: 10.1016/j.tics.2012.06.013

Costello, P., Jiang, Y., Baartman, B., McGlennen, K., and He, S. (2009). Semantic and subword priming during binocular suppression. *Conscious. cogn.* 18, 375–382. doi: 10.1016/j.concog.2009.02.003

---

[5] One can also combine these two measures in a multiple-alternative forced choice task, in which each alternative corresponds to one objective response associated with a subjective level of visibility (for instance, letters of different sizes in which the letter type indicates the category of a stimulus, and its size indicates the confidence with which the decision is made).

Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J.-F., Poline, J.-B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nat. Neurosci.* 4, 752–758. doi: 10.1038/89551

de Zilva, D., Vu, L., Newell, B. R., and Pearson, J. (2013). Exposure is not enough: suppressing stimuli from awareness can abolish the mere exposure effect. *PLoS ONE* 8:e77726. doi: 10.1371/journal.pone.0077726

Faivre, N., Berthet, V., and Kouider, S. (2012a). Nonconscious influences from emotional faces: a comparison of visual crowding, masking, and continuous flash suppression. *Front. Psychol.* 3:129. doi: 10.3389/fpsyg.2012.00129

Faivre, N., Charron, S., Roux, P., Lehéricy, S., and Kouide, S. (2012b). Nonconscious emotional processing involve distinct neural pathways for pictures and videos. *Neuropsychologia* 50, 3736–3744. doi: 10.1016/j.neuropsychologia.2012.10.025

Faivre, N., and Koch, C. (2014a). Inferring the direction of implied motion depends on visual awareness. *J. Vis.* 14, 1–14. doi: 10.1167/14.4.4

Faivre, N., and Koch, C. (2014b). Temporal structure coding with and without awareness. *Cognition* 131, 401–414. doi: 10.1016/j.cognition.2014.02.008

Faivre, N., and Kouider, S. (2011a). Increased sensory evidence reverses nonconscious priming during crowding. *J. Vis.* 11, 1–13. doi: 10.1167/11.13.16

Faivre, N., and Kouider, S. (2011b). Multi-Feature objects elicit nonconscious priming despite crowding. *J. Vis.* 11, 1–10. doi: 10.1167/11.3.2

Fang, F., and He, S. (2005). Cortical responses to invisible objects in human dorsal and ventral pathways. *Nat. Neurosci.* 8, 1380–1385. doi: 10.1038/nn1537

Fang, F., and He, S. (2008). Crowding alters the spatial distribution of attention modulation in human primary visual cortex. *J. Vis.* 8, 6.1–6.9. doi: 10.1167/8.9.6

Fischer, J., and Whitney, D. (2011). Object-level visual information gets through the bottleneck of crowding. *J. Neurophysiol.* 106, 1389–1398. doi: 10.1152/jn.00904.2010

Gayet, S., Van Der Stigchel, S., and Paffen, C. (2014). Breaking continuous flash suppression: competing for consciousness on the pre-semantic battlefield. *Front. Psychol.* 5:460. doi: 10.3389/fpsyg.2014.00460

Goodale, M. A., and Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends Neurosci.* 15, 20–25. doi: 10.1016/0166-2236(92)90344-8

Gray, K. L., Adams, W. J., Hedger, N., Newton, K. E., and Garner, M. (2013). Faces and awareness: low-level, not emotional factors determine perceptual dominance. *Emotion* 13, 537. doi: 10.1037/a0031403

Haberman, J., and Whitney, D. (2007). Rapid extraction of mean emotion and gender from sets of faces. *Curr. Biol.* 17, R751–R753. doi: 10.1016/j.cub.2007.06.039

Haberman, J., and Whitney, D. (2009). Seeing the mean: ensemble coding for sets of faces. *J. Exp. Psychol. Hum. Percept. Perform.* 35, 718–734. doi: 10.1037/a0013899

Harris, J. J., Schwarzkopf, D. S., Song, C., Bahrami, B., and Rees, G. (2011). Contextual illusions reveal the limit of unconscious visual processing. *Psychol. Sci.* 22, 399–405. doi: 10.1177/0956797611399293

Hassin, R. R. (2013). Yes it can on the functional abilities of the human unconscious. *Perspect. Psychol. Sci.* 8, 195–207. doi: 10.1177/1745691612460684

He, S., Cavanagh, P., and Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature* 383, 334–337. doi: 10.1038/383334a0

Hebart, M., and Hesselmann, G. (2012). What visual information is processed in the human dorsal stream? *J. Neurosci.* 32, 8107–8109. doi: 10.1523/JNEUROSCI.1462-12.2012

Hesselmann, G., and Malach, R. (2011). The link between fMRI-BOLD activation and perceptual awareness is "stream-invariant" in the human visual system. *Cereb. Cortex* 21, 2829–2837. doi: 10.1093/cercor/bhr085

Heyman, T., and Moors, P. (2012). Using interocular suppression and EEG to study semantic processing. *J. Neurosci.* 32, 1515–1516. doi: 10.1523/JNEUROSCI.5726-11.2012

Hong, S. W., and Blake, R. (2009). Interocular suppression differentially affects achromatic and chromatic mechanisms. *Atten. Percept. Psychophys.* 71, 403–411. doi: 10.3758/APP.71.2.403

Hussain, Z., Webb, B. S., Astle, A. T., and McGraw, P. V. (2012). Perceptual learning reduces crowding in amblyopia and in the normal periphery. *J. Neurosci.* 32, 474–480. doi: 10.1523/JNEUROSCI.3845-11.2012

Jiang, Y., Costello, P., Fang, F., Huang, M., and He, S. (2006). A gender-and sexual orientation-dependent spatial attentional effect of invisible images. *Proc. Natl. Acad. Sci. U.S.A.* 103, 17048–17052. doi: 10.1073/pnas.0605678103

Jiang, Y., Costello, P., and He, S. (2007). Processing of invisible stimuli: advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychol. Sci.* 18, 349–355. doi: 10.1111/j.1467-9280.2007.01902.x

Jiang, Y., and He, S. (2006). Cortical responses to invisible faces: dissociating subsystems for facial-information processing. *Curr. Biol.* 16, 2023–2029. doi: 10.1016/j.cub.2006.08.084

Jiang, Y., Shannon, R. W., Vizueta, N., Bernat, E. M., Patrick, C. J., and He, S. (2009). Dynamics of processing invisible faces in the brain: automatic neural encoding of facial expression information. *Neuroimage* 44, 1171–1177. doi: 10.1016/j.neuroimage.2008.09.038

Kanai, R., Tsuchiya, N., and Verstraten, F. A. J. (2006). The scope and limits of top-down attention in unconscious visual processing. *Curr. Biol.* 16, 2332–2336. doi: 10.1016/j.cub.2006.10.001

Kanai, R., Walsh, V., and Tseng, C. H. (2010). Subjective discriminability of invisibility: a framework for distinguishing perceptual and attentional failures of awareness. *Conscious. Cogn.* 19, 1045–1057. doi: 10.1016/j.concog.2010.06.003

Kang, M.-S., Blake, R., and Woodman, G. F. (2011). Semantic analysis does not occur in the absence of awareness induced by interocular suppression. *J. Neurosci.* 31, 13535–13545. doi: 10.1523/JNEUROSCI.1691-11.2011

Kaunitz, L., Fracasso, A., and Melcher, D. (2011). Unseen complex motion is modulated by attention and generates a visible aftereffect. *J. Vis.* 11, 10. doi: 10.1167/11.13.10

Kim, C. Y., and Blake, R. (2005). Psychophysical magic: rendering the visible invisible. *Trends Cogn. Sci.* 9, 381–388. doi: 10.1016/j.tics.2005.06.012

Koch, C., and Tsuchiya, N. (2007). Attention and consciousness: two distinct brain processes. *Trends Cogn. Sci.* 11, 16–22. doi: 10.1016/j.tics.2006.10.012

Kooi, F. L., Toet, A., Tripathy, S. P., and Levi, D. M. (1994). The effect of similarity and duration on spatial interaction in peripheral vision. *Spat. Vis.* 8, 255–279. doi: 10.1163/156856894X00350

Kouider, S., and Dupoux, E. (2004). Partial awareness creates the "illusion" of subliminal semantic priming. *Psychol. sci.* 15, 75–81. doi: 10.1111/j.0963-7214.2004.01502001.x

Kouider, S., Berthet, V., and Faivre, N. (2011). Preference is biased by crowded facial expressions. *Psychol. Sci.* 22, 184–189. doi: 10.1177/0956797610396226

Kouider, S., de Gardelle, V., Sackur, J., and Dupoux, E. (2010). How rich is consciousness? The partial awareness hypothesis. *Trends Cogn. Sci.* 14, 301–307. doi: 10.1016/j.tics.2010.04.006

Kouider, S., and Dehaene, S. (2007). Levels of processing during non-conscious perception: a critical review of visual masking. *Philos. Trans. R. Soc. B Biol. Sci.* 362, 857–875. doi: 10.1098/rstb.2007.2093

Lamme, V. A. F. (2003). Why visual attention and awareness are different. *Trends Cogn. Sci.* 7, 12–18. doi: 10.1016/S1364-6613(02)00013-X

Lapate, R. C., Rokers, B., Li, T., and Davidson, R. J. (2013). Nonconscious emotional activation colors first impressions a regulatory role for conscious awareness. *Psychol. Sci.* 25, 349–357. doi: 10.1177/0956797613503175

Lau, J. S. F., and Cheung, S. H. (2012). Illusory contour formation survives crowding. *J. Vis.* 12, 15. doi: 10.1167/12.6.15

Lehmkuhle, S. W., and Fox, R. (1975). Effect of binocular rivalry suppression on the motion aftereffect. *Vision Res.* 15, 855–859. doi: 10.1016/0042-6989(75)90266-7

Levi, D. M. (2008). Crowding – an essential bottleneck for object recognition: a mini-review. *Vision Res.* 48, 635–654. doi: 10.1016/j.visres.2007.12.009

Lin, Z., and He, S. (2009). Seeing the invisible: the scope and limits of unconscious processing in binocular rivalry. *Prog. Neurobiol.* 87, 195–211. doi: 10.1016/j.pneurobio.2008.09.002

Livne, T., and Sagi, D. (2007). Configuration influence on crowding. *J. Vis.* 7, 4.1–4.12. doi: 10.1167/7.2.4

Livne, T., and Sagi, D. (2010). How do flankers' relations affect crowding? *J. Vis.* 10, 1.1–1.14. doi: 10.1167/10.3.1

Ludwig, K., Kathmann, N., Sterzer, P., Franz, V. H., and Hesselmann, G. (2013). Learning to detect but not to grasp suppressed visual stimuli. *Neuropsychologia* 51, 2930–2938. doi: 10.1016/j.neuropsychologia.2013.09.035

Lupyan, G., and Ward, E. J. (2013). Language can boost otherwise unseen objects into visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* 110, 14196–14201. doi: 10.1073/pnas.1303312110

Manassi, M., Sayim, B., and Herzog, M. H. (2012). Grouping, pooling, and when bigger is better in visual crowding. *J. Vis.* 12, 13. doi: 10.1167/12.10.13

Maruya, K., Watanabe, H., and Watanabe, M. (2008). Adaptation to invisible motion results in low-level but not high-level aftereffects. *J. Vis.* 8, 7.1–7.11. doi: 10.1167/8.11.7

Montaser-Kouhsari, L., and Rajimehr, R. (2005). Subliminal attentional modulation in crowding condition. *Vision Res.* 45, 839–844. doi: 10.1016/j.visres.2004.10.020

Moradi, F., Koch, C., and Shimojo, S. (2005). Face adaptation depends on seeing the face. *Neuron* 45, 169–175. doi: 10.1016/j.neuron.2004.12.018

Mudrik, L., Breska, A., Lamy, D., and Deouell, L. Y. (2011). Integration without awareness: expanding the limits of unconscious processing. *Psychol. Sci.* 22, 764–770. doi: 10.1177/0956797611408736

Mudrik, L., Gelbard-Sagiv, H., Faivre, N., and Koch, C. (2013). Knowing where without knowing what: partial awareness and high-level processing in continuous flash suppression. *J. Vis.* 13, 1103–1103. doi: 10.1167/13.9.1103

Nguyen, V. A., Freeman, A. W., and Alais, D. (2003). Increasing depth of binocular rivalry suppression along two visual pathways. *Vision Res.* 43, 2003–2008. doi: 10.1016/S0042-6989(03)00314-6

O'Shea, R. P., and Crassini, B. (1981). Interocular transfer of the motion after-effect is not reduced by binocular rivalry. *Vision Res.* 21, 801–804. doi: 10.1016/0042-6989(81)90177-2

Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., and Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nat. Neurosci.* 4, 739–744. doi: 10.1038/89532

Pelli, D. G., and Tillman, K. A. (2008). The uncrowded window of object recognition. *Nat. Neurosci.* 11, 1129–1135. doi: 10.1038/nn.2187

Peng, C., Zhang, Y., Chen, Y., and Zhang, M. (2013). Crowded words can be processed semantically: evidence from an ERP study. *Int. J. of Psychophysiol.* 88, 91–95. doi: 10.1016/j.ijpsycho.2013.03.002

Pizzi, D., Kosunen, I., Viganó, C., Polli, A. M., Ahmed, I., Zanella, D., et al. (2012). "Incorporating subliminal perception in synthetic environments," in *Proceedings of the 2012 ACM Conference on Ubiquitous Computing*, (New York: ACM), 1139–1144. doi: 10.1145/2370216.2370458

Raio, C. M., Carmel, D., Carrasco, M., and Phelps, E. A. (2012). Nonconscious fear is quickly acquired but swiftly forgotten. *Curr. Biol.* 22, R477–R479. doi: 10.1016/j.cub.2012.04.023

Rajimehr, R., Vaziri-Pashkam, M., Afraz, S.-R., and Esteky, H. (2004). Adaptation to apparent motion in crowding condition. *Vision Res.* 44, 925–931. doi: 10.1016/j.visres.2003.11.020

Ramsøy, T., and Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenol. Cogn. Sci.* 3, 1–23. doi: 10.1023/B:PHEN.0000041900.30172.e8

Roseboom, W., and Arnold, D. H. (2011). Learning to reach for 'invisible' visual input. *Curr. Biol.* 21, R493–R494. doi: 10.1016/j.cub.2011.05.036

Rosenthal, R. (1979). The file drawer problem and tolerance for null results. *Psychol. Bull.* 86, 638–641. doi: 10.1037/0033-2909.86.3.638

Rothkirch, M., Stein, T., Sekutowicz, M., and Sterzer, P. (2012). A direct oculomotor correlate of unconscious visual processing. *Curr. Biol.* 22, R514–R515. doi: 10.1016/j.cub.2012.04.046

Saarela, T. P., Sayim, B., Westheimer, G., and Herzog, M. H. (2009). Global stimulus configuration modulates crowding. *J. Vis.* 9, 5. doi: 10.1167/9.2.5

Sakuraba, S., Sakai, S., Yamanaka, M., Yokosawa, K., and Hirayama, K. (2012). Does the human dorsal stream really process a category for tools? *J. Neurosci.* 32, 3949–3953. doi: 10.1523/JNEUROSCI.3973-11.2012

Sandberg, K., Timmermans, B., Overgaard, M., and Cleeremans, A. (2010). Measuring consciousness : is one measure better than the other ? *Conscious. Cogn.* 19, 1069–1078. doi: 10.1016/j.concog.2009.12.013

Sergent, C., and Dehaene, S. (2004). Is consciousness a gradual phenomenon? Evidence for an all-or-none bifurcation during the attentional blink. *Psychol. Sci.* 15, 720–728. doi: 10.1111/j.0956-7976.2004.00748.x

Seth, A. K., Dienes, Z., Cleeremans, A., Overgaard, M., and Pessoa, L. (2008). Measuring consciousness : relating behavioural and neurophysiological approaches. *Trends Cogn. Sci.* 12, 314–321. doi: 10.1016/j.tics.2008.04.008

Sklar, A. Y., Levy, N., Goldstein, A., Mandel, R., Maril, A., and Hassin, R. R. (2012). Reading and doing arithmetic nonconsciously. *Proc. Natl. Acad. Sci. U.S.A.* 109, 19614–19619. doi: 10.1073/pnas.1211645109

Stein, T., Hebart, M. N., and Sterzer, P. (2011). Breaking continuous flash suppression: a new measure of unconscious processing during interocular suppression? *Front. Hum. Neurosci.* 5:167. doi: 10.3389/fnhum.2011.00167

Stein, T., Seymour, K., Hebart, M. N., and Sterzer, P. (2013). Rapid fear detection relies on high spatial frequencies. *Psychol. Sci.* 25, 566–574. doi: 10.1177/0956797613512509

Stein, T., and Sterzer, P. (2011). High-level face shape adaptation depends on visual awareness: evidence from continuous flash suppression. *J. Vis.* 11, 5. doi: 10.1167/11.8.5

Stein, T., and Sterzer, P. (2014). Unconscious processing under interocular suppression: getting the right measure. *Front. Psychol.* 5:387. doi: 10.3389/fpsyg.2014.00387

Stein, T., Sterzer, P., and Peelen, M. V. (2012). Privileged detection of conspecifics: evidence from inversion effects during continuous flash suppression. *Cognition* 125, 64–79. doi: 10.1016/j.cognition.2012.06.005

Sterzer, P., Haynes, J.-D., and Rees, G. (2008). Fine-scale activity patterns in high-level visual areas encode the category of invisible objects. *J. Vis.* 8, 10.1–10.12. doi: 10.1167/8.15.10

Sterzer, P., Jalkanen, L., and Rees, G. (2009). Electromagnetic responses to invisible face stimuli during binocular suppression. *Neuroimage* 46, 803–808. doi: 10.1016/j.neuroimage.2009.02.046

Sterzer, P., Stein, T., Rothkirch, M., and Hesselmann, G. (2014). Neural processing of visual information under interocular suppression: A critical review. *Front. Psychol.* 5:453. doi: 10.3389/fpsyg.2014.00453

Stewart, L. H., Ajina, S., Getov, S., Bahrami, B., Todorov, A., and Rees, G. (2012). Unconscious evaluation of faces on social dimensions. *J. Exp. Psychol. Gen.* 141, 715. doi: 10.1037/a0027950

Suchow, J. W., and Pelli, D. G. (2013). Learning to detect and combine the features of an object. *Proc. Natl. Acad. Sci. U.S.A.* 110, 785–790. doi: 10.1073/pnas.1218438110

Sun, G. J., Chung, S. T. L., and Tjan, B. S. (2010). Ideal observer analysis of crowding and the reduction of crowding through learning. *J. Vis.* 10, 16. doi: 10.1167/10.5.16

Tamietto, M., and de Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nat. Rev. Neurosci.* 11, 697–709. doi: 10.1038/nrn2889

Tripathy, S. P., and Cavanagh, P. (2002). The extent of crowding in peripheral vision does not scale with target size. *Vision Res.* 42, 2357–2369. doi: 10.1016/S0042-6989(02)00197-9

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Tsuchiya, N., Koch, C., Gilroy, L. A., and Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *J. Vis.* 6, 1068–1078. doi: 10.1167/6.10.6

Tsuchiya, N., Moradi, F., Felsen, C., Yamazaki, M., and Adolphs, R. (2009). Intact rapid detection of fearful faces in the absence of the amygdala. *Nat. Neurosci.* 12, 1224–1225. doi: 10.1038/nn.2380

Tsuchiya, N., and van Boxtel, J. (2013). Introduction to research topic: attention and consciousness in different senses. *Front. Psychol.* 4:249. doi: 10.3389/fpsyg.2013.00249

van den Berg, R., Roerdink, J. B. T. M., and Cornelissen, F. W. (2007). On the generality of crowding: visual crowding in size, saturation, and hue compared to orientation. *J. Vis.* 7, 1–11. doi: 10.1167/7.2.14

Vizueta, N., Patrick, C. J., Jiang, Y., Thomas, K. M., and He, S. (2012). Dispositional fear, negative affectivity, and neuroimaging response to visually suppressed emotional faces. *Neuroimage* 59, 761–771. doi: 10.1016/j.neuroimage.2011.07.015

Wade, N. J., and Wenderoth, P. (1978). The influence of colour and contour rivalry on the magnitude of the tilt after-effect. *Vision Res.* 18, 827–835. doi: 10.1016/0042-6989(78)90123-2

Wang, L., Weng, X., and He, S. (2012). Perceptual grouping without awareness: superiority of Kanizsa triangle in breaking interocular suppression. *PLoS ONE* 7:e40106. doi: 10.1371/journal.pone.0040106

Watanabe, M., Cheng, K., Murayama, Y., Ueno, K., Asamizuya, T., Tanaka, K., et al. (2011). Attention but not awareness modulates the BOLD signal in the human V1 during binocular suppression. *Science* 334, 829–831. doi: 10.1126/science.1203161

Weisstein, N., and Haber, R. N. (1965). A u-shaped backward masking function in vision. *Psychon. Sci.* 2, 75–76. doi: 10.3758/BF03343337

White, K. D., Petry, H. M., Riggs, L. A., and Miller, J. (1978). Binocular interactions during establishment of McCollough effects. *Vision Res.* 18, 1201–1215. doi: 10.1016/0042-6989(78)90105-0

Whitney, D. (2005). Motion distorts perceived position without awareness of motion. *Curr. Biol.* 15, R324–R326. doi: 10.1016/j.cub.2005.04.043

Whitney, D., and Levi, D. M. (2011). Visual crowding: a fundamental limit on conscious perception and object recognition. *Trends Cogn. Sci.* 15, 160–168. doi: 10.1016/j.tics.2011.02.005

Yang, E., Zald, D. H., and Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion* 7, 882. doi: 10.1037/1528-3542.7.4.882

Yang, E., and Blake, R. (2012). Deconstructing continuous flash suppression. *J. Vis.* 12, 8. doi: 10.1167/12.3.8

Yang, Y. H., and Yeh, S. L. (2011). Accessing the meaning of invisible words. *Conscious. cogn.* 20, 223–233. doi: 10.1016/j.concog.2010.07.005

Yang, E., Hong, S.-W., and Blake, R. (2010). Adaptation aftereffects to facial expressions suppressed from visual awareness. *J. Vis.* 10, 24. doi: 10.1167/10.12.24

Yeh, S.-L., He, S., and Cavanagh, P. (2012). Semantic priming from crowded words. *Psychol. Sci.* 23, 608–616. doi: 10.1177/0956797611434746

Yeshurun, Y., and Rashal, E. (2010). Precueing attention to the target location diminishes crowding and reduces the critical distance. *J. Vis.* 10, 16. doi: 10.1167/10.10.16

Yuval-Greenberg, S., and Heeger, D. J. (2013). Continuous flash suppression modulates cortical activity in early visual cortex. *J. Neurosci.* 33, 9635–9643. doi: 10.1523/JNEUROSCI.4612-12.2013

Zabelina, D. L., Guzman-Martinez, E., Ortega, L., Grabowecky, M., Suzuki, S., and Beeman, M. (2013). Suppressed semantic information accelerates analytic problem solving. *Psychon. Bull. Rev.* 20, 581–585. doi: 10.3758/s13423-012-0364-1

Zadbood, A., Lee, S.-H., and Blake, R. (2011). Stimulus fractionation by interocular suppression. *Front. Hum. Neurosci.* 5:135. doi: 10.3389/fnhum.2011.00135

Zhou, G., Zhang, L., Liu, J., Yang, J., and Qu, Z. (2010). Specificity of face processing without awareness. *Conscious. Cogn.* 19, 408–412. doi: 10.1016/j.concog.2009.12.009

Zimba, L. D., and Blake, R. (1983). Binocular rivalry and semantic processing: out of sight, out of mind. *J. Exp. Psychol. Hum. Percept. Perform.* 9, 807–815. doi: 10.1037//0096-1523.9.5.807

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 12 February 2014; accepted: 01 May 2014; published online: 27 May 2014.
Citation: Faivre N, Berthet V and Kouider S (2014) Sustained invisibility through crowding and continuous flash suppression: a comparative review. Front. Psychol. ***5****:475. doi: 10.3389/fpsyg.2014.00475*
This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

HYPOTHESIS AND THEORY ARTICLE
published: 17 September 2014
doi: 10.3389/fpsyg.2014.00975

Invisibility and interpretation

Michael H. Herzog[1]*, **Frouke Hermens**[2] **and Haluk Öğmen**[3]

[1] Brain Mind Institute, Ecole Polytechnique Fédérale de Lausanne (EPFL), Lausanne, Switzerland
[2] School of Psychology, University of Aberdeen, Aberdeen, UK
[3] Department of Electrical and Computer Engineering, Center for NeuroEngineering and Cognitive Science, University of Houston, Houston, TX, USA

Edited by:
Julien Dubois, California Institute of Technology, USA

Reviewed by:
Niko Busch, Charité - Universitätsmedizin Berlin, Germany
Filipp Schmidt, University of Kaiserslautern, Germany
Martin Nikolai Hebart, University Medical Center Hamburg-Eppendorf, Germany

***Correspondence:**
Michael H. Herzog, Ecole Polytechnique Fédérale de Lausanne (EPFL), Station 19, CH-1015 Lausanne, Switzerland
e-mail: michael.herzog@epfl.ch

Invisibility is often thought to occur because of the low-level limitations of the visual system. For example, it is often assumed that backward masking renders a target invisible because the visual system is simply too slow to resolve the target and the mask separately. Here, we propose an alternative explanation in which invisibility is a goal rather than a limitation and occurs naturally when making sense out of the plethora of incoming information. For example, we present evidence that (in)visibility of an element can strongly depend on how it groups with other elements. Changing grouping changes visibility. In addition, we will show that features often just appear to be invisible but are in fact visible in a way the experimenter is not aware of.

Keywords: masking, priming, visibility, consciousness

1. INTRODUCTION

It is often assumed that invisibility reflects fundamental limitations of the human visual system and, vice versa, any stimulus that is above these limitations becomes automatically visible. For example, objects that are too small with respect to the spatial resolution of the visual system are invisible but can be clearly perceived after magnification by a microscope. However, there are interesting cases where a stimulus is visible when presented alone but becomes invisible when it is presented with other stimuli. Here, the stimulus itself is clearly above the basic resolution limits of the visual system. There are two cases. The first case is based on rather low-level "irreversible" automatic mechanisms. For example, a clearly visible but faint line becomes invisible in the neighborhood of a high luminance patch because of gain control. Similarly, the stars are invisible during the day because the bright sunlight drives the rod system into saturation. In these cases, invisibility occurs because of adjusting the dynamic range of the visual system to that of the environment. However, we claim that there are many situations, frequently used in consciousness research and many other fields, where invisibility is not caused by such low-level– and irreversible– factors, in the sense that "flexible" changes in context can lead to drastic changes in visibility. Here, we show evidence for this second type of invisibility by the example of visual masking but argue that similar processes of Gestalt formation play a central role for (in)visibility in general.

In masked priming studies, a target is followed by a mask (Klotz and Neumann, 1999; Schmidt, 2002; Vorberg et al., 2003). In a first condition, observers are asked to discriminate the features of the target (direct measure). If parameters of the target and mask are well chosen, performance on the target is at or close to chance level, i.e., its features are unconscious and invisible. Still, the features of the target can *prime* response times when observers discriminate, in a second condition, features of the mask (indirect measure). We like to mention that in most of these studies only the *features* of the target are unconscious, and not the target *itself*. The priming effects are often explained by pre-activation of the motor system (e.g., Klotz and Neumann, 1999; Schmidt, 2002; Vorberg et al., 2003). In a fast, unconscious processing sweep, the target pre-activates the motor cortex, which leads to speeded or slowed processing when the task is on the mask. Support for this motor pre-activation comes from many behavioral (Schmidt, 2002) and ERP studies (e.g., Eimer and Schlaghecken, 2000). However, why are the target features invisible at all? Invisibility is usually thought to occur because of the limitations of the visual system. For example in integration masking, it is assumed that target and mask integrate into *one* conglomerate because the visual system cannot separate the two stimuli due to its limited temporal resolution. Integration may well occur as early as on the retinal level and can be seen as a superposition of the target and mask, similar to when two slides are projected together (e.g., Di Lollo, 1980; Kahneman, 1968; Scheerer, 1973). Hence, invisibility occurs because the system is at its temporal limits. Other mechanisms rely on different types of masking and other types of low level mechanisms such as in metacontast masking (see Discussion).

Here, we show evidence that invisibility is often not the outcome of limitations of the visual system. Instead, we argue that invisibility is due to purposeful interpretation, i.e., a goal rather than a limitation. Visibility and invisibility depend on how elements group and occur naturally and necessarily because of the ill-posed problems of vision.

2. REVIEW OF EVIDENCE

2.1. EXCELLENT TEMPORAL PRECISION

Consider the situation in **Figure 1A**. A right offset vernier is followed immediately by a left offset vernier or vice versa. An almost aligned vernier is perceived, a phenomenon called feature fusion (Efron, 1967; Herzog et al., 2003). Participants cannot perceive the individual verniers[1]. This outcome is classically explained by integration masking where the two verniers are invisible because of a lack of temporal resolution (Scheerer, 1973; Turvey, 1973). The human brain is simply not *able* to render the two elements visible individually.

However, this is not the case. When we presented an array of 25 verniers in the second frame, the first vernier became visible and discrimination of its offset was only slightly deteriorated compared to when presented alone (**Figures 1B,C**; Hermens et al., 2009). Hence, even though the two central verniers are identical to the feature fusion condition, the human brain can now easily resolve the two verniers and their offsets. We propose that the 25 verniers are grouped as *one* array of elements independently of the first vernier, which is thus rendered visible as an element in its own right (Herzog and Koch, 2001; Herzog and Fahle, 2002; Ghose et al., 2013). In line with this proposition, the offset direction of the 25 verniers has almost no influence, i.e., performance is roughly the same when the 25 verniers are offset in the opposite direction than the first vernier or not offset at all (Hermens et al., 2009). Spatial grouping of the vernier array prevents the *temporal* integration of the first and second vernier, even though

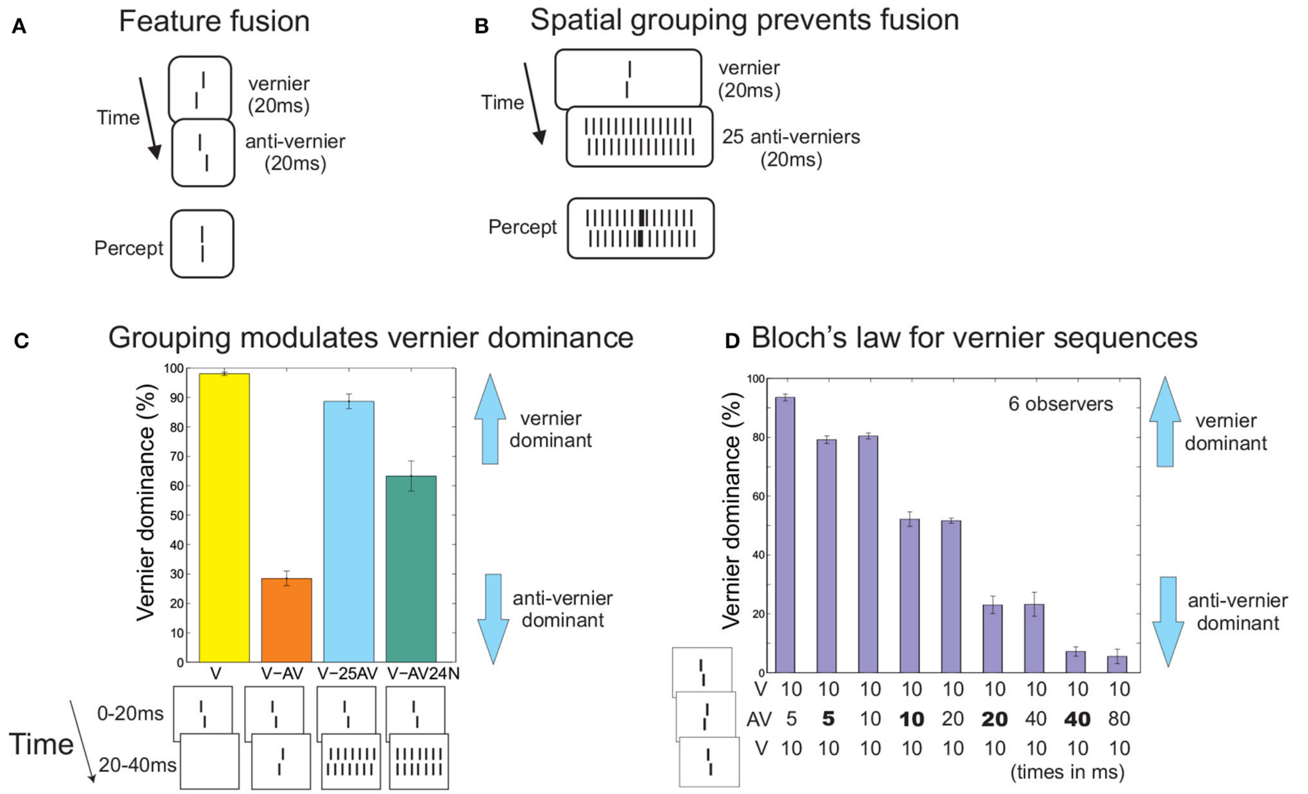


FIGURE 1 | (A) Feature fusion. A right or left vernier (V) is followed by a second vernier with an opposite offset direction (anti-vernier, AV). Only one vernier with an almost aligned offset is perceived. Observers cannot tell whether the first or second vernier is offset to the right. Hence, the verniers themselves are unconscious (direct measure of awareness). **(B)** When the second vernier is flanked by 12 copies of itself on each side, temporal feature fusion almost completes ceases. The first vernier becomes visible as an element in its own right, appearing to be superimposed on the grating of 25 anti-verniers. **(C)** To give quantitative expression, we determined vernier dominance. In each trial, we determined whether the response of the observers matched the offset direction of the first vernier. Hence, a 100% score means that observers pushed always the button according to the first vernier. A 0% score means observers decided always according to the second vernier, and for 50% both verniers contributed equally on average. Performance is at ceiling for a single vernier (V). Adding the anti-vernier leads to anti-vernier dominance (in accordance with the fact that in fusion, the latter element dominates). When there are 2*12 copies of the second vernier, the first vernier becomes visible and performance is almost as good as for the single vernier (V-25AV; only 2*6 verniers are shown here). Locally, at the center, the very same first and second vernier are presented as in the previous conditions. Performance is roughly independent of whether or not these verniers are offset or aligned indicating again that there is no temporal fusion (V-AV24N). We argue that spatial integration trumps temporal fusion. Visibility of the first vernier depends on grouping and not on low level limitations. Data from Hermens et al. (2009). **(D)** Bloch's law for 3-vernier sequences. Doubling the luminance of the anti-vernier has the same effect as doubling its duration (doubled luminances are indicated by bold font). Data from Scharnowski et al. (2007a).

---

[1] Note that if the offsets of the verniers are large, one can see four line segments instead of two, while for intermediate offsets, motion is perceived, see Figure 1 in Scharnowski et al. (2007b). Here the vernier offsets are kept small enough so as to have fusion of the two verniers.

both are presented at the same retinal location in both conditions. This suggests that (in)visibility depends crucially on perceptual grouping.

Next, we show that the integration of vernier offsets is extremely precise, meaning that while participants cannot report the individual verniers, information about their individual offsets, durations and luminance is still preserved. We presented three verniers in immediate succession. The first and last vernier had always the same offset direction (left or right), whereas the second vernier was offset in the opposite direction. Presentation time was 10 ms for the first and last vernier, and varied for the second vernier. When the second vernier's duration was 5 ms, performance was strongly determined by the first (and third) vernier (**Figure 1D**). When we doubled the luminance of the second vernier, still presented for 5 ms, it contributed more strongly to performance (**Figure 1D**), meaning that although participants could not tell how many verniers were presented and of what luminance, the brain still incorporates this information. Performance remained on this level when we increased the duration to 10 ms but reduced the luminance to normal. Hence, increasing/decreasing the duration can be compensated by decreasing/increasing the luminance. Feature fusion follows precisely Bloch's law, which states that brightness is the product of luminance times duration (Scharnowski et al., 2007a). Hence, we have shown that even though the individual vernier offsets are invisible, the human brain carefully analyzes and integrates them into one offset, which in turn is consciously perceived. This means that in feature fusion, the outputs of specific feature detectors (vernier offsets) are combined into a meaningful percept, depending on perceptual grouping. This is very different from integration masking, in which integration results in a "pixel-by-pixel" conglomerate of the target and the mask (on the retinal level), similar to when two slides are projected together superimposed.

Here is another illustration of why feature fusion differs fundamentally from integration masking. In the case of feature fusion with the two verniers (**Figure 1C**), performance is close to the 50% level with a slight dominance of the second vernier. This result may be taken as chance level performance because of integration masking (the superposition of a first right and second left vernier is the same as the other way around and, hence, observers cannot discriminate the two situations). However, as we have argued, the 50% level just shows that the two vernier offsets are equally weighted in the integration. Performance quickly changes from 50% when one of the verniers has a slightly higher luminance (or offset size). Similar results were found for complex sequences of verniers (Hermens et al., 2010).

Feature fusion occurs also in other visual domains. For example, when a red disk is followed by a green disk, only one yellow disk is perceived (Efron, 1967, 1973). Also here, while the individual elements (the disks) are not visible to the participants, the features of the elements are still registered by the brain and combined into *one* perceived object.

2.2. UNCONSCIOUSNESS AND LONG LASTING FEATURE INTEGRATION

Up to now, we have provided evidence that invisibility can be the result of grouping rather than of low level limitations of the visual system. Here, we show, first, that the vernier offsets are indeed unconscious. Second, the unconscious offsets are represented in the visual system for an extensive duration (of around 420 ms) even though the individual stimuli (vernier and anti-vernier) are presented for a short time (30 ms each).

We presented a vernier and the anti-vernier, as above. Observers were told about the set-up and asked whether the first or second vernier is offset to the right (Scharnowski et al., 2009). Performance was at about 52%, i.e., almost at chance level. As an aside note, we use two direct measures to test for unconsciousness ("which vernier is offset to the right" and "what is the conscious, fused vernier offset") rather than a direct and an indirect one (based on reaction times, as in priming studies, e.g., Schmidt, 2002; Vorberg et al., 2003).

Next, we show that the unconscious vernier offsets are not only carefully analyzed and integrated but that this process lasts for up to 420 ms after stimulus onset. We presented the first and second vernier for 30 ms each. We adjusted the second vernier offset such that dominance was at about 50% for each participant. Hence, both verniers contributed equally to feature fusion (**Figure 2**). Next, we applied Transcranial Magnetic Stimulation (TMS) at various stimulus onset asynchronies (SOAs) over the occipital lobe. For SOAs up to 120 ms, TMS led to dominance of the second vernier. From 120 to 420 ms, the first vernier dominated. The most important conclusion from this finding is that the two verniers cannot be fully integrated before 420 ms for the following reason. By design, both verniers contribute equally to fusion in the basic no-TMS-condition. When the verniers were integrated immediately, TMS could only modulate the combined representation but not favor one vernier over the other. The trick of the experiment is that the 50% dominance level (equal contribution of both verniers to fusion) and chance level performance are the same. In this sense, whatever the effect of TMS on the integrated representation is, discrimination of its offset remains at chance (similar to the outcome when observers would close their eyes). Now by the converse argument, if performance is *not* at 50%, TMS "favors" one vernier over the other and hence the two cannot be fully integrated, i.e., there are separate representations for the two verniers for at least 420 ms (Scharnowski et al., 2009). As an implication, this experiment provides evidence that conscious access to feature information in our paradigm cannot emerge before 420 ms, since the vernier offsets themselves are unconsciousness as shown above.

We like to add that vernier fusion, as well as color and motion fusion, can be manipulated also by light masks, instead of TMS (Pilz et al., 2013).

2.3. FEATURE INTEGRATION ACROSS SPACE AND TIME

Up to now, we have shown that, first, whether an element is rendered visible or invisible can crucially depend on perceptual grouping. In these instances, invisibility cannot be explained by limited temporal resolution or other low-level mechanisms. Second, we have provided evidence that features even of invisible elements are carefully registered and, depending on grouping, integrated with other elements. Third, we have shown that unconscious feature integration can be a long lasting process. Using TMS, we found that consciousness does not emerge before 420 ms.

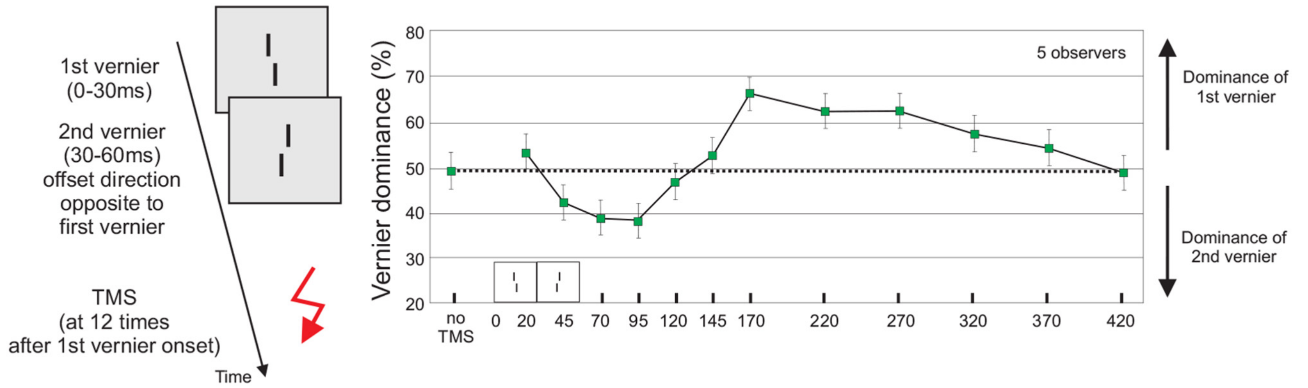


FIGURE 2 | The influence of TMS on feature fusion. A sequence of a vernier and an anti-vernier is followed by a TMS-pulse to the occipital cortex. The offsets of the vernier and anti-vernier are adjusted so that for each participant, vernier dominance is at 50% without TMS (dotted line). TMS applied at SOAs 20–120 ms leads to dominance of the second vernier, TMS applied at SOAs 120–420 ms leads to dominance of the first vernier. The long-lasting TMS effect indicates that feature integration cannot be completed before 420 ms. Figure adapted from Scharnowski et al. (2009). The arrow indicates the TMS pulse.

The question arises, why is feature integration so long lasting? Why is there is such a long period of unconsciousness? Here, we will suggest that the brain needs to integrate information across extended periods because we and the world are in permanent motion. In addition, we will show that features of an invisible element can be rendered visible at other elements. Hence, features of elements can be transported across space.

We presented a left or right offset vernier as the first element, followed by a sequence of *aligned* verniers (**Figure 3**). Two expanding streams of lines are perceived originating from the center of the screen (sequential metacontrast, Otto et al., 2006). The first vernier is rendered unconscious. To show this, we presented the sequence with and without the vernier in two subsequent intervals. Observers indicated whether the vernier was present or absent (direct measure). Performance was close to chance level. Surprisingly, however, the vernier offset is visible at the flankers even though the flankers are aligned and the vernier itself is invisible (feature inheritance; Herzog and Koch, 2001; Sharikadze et al., 2005). In quantitative experiments, observers could well discriminate whether the offset is to the left or right (second direct measure; **Figure 3**). When one or more of the flanking lines are offset themselves, the target and flanker offsets integrate as in feature fusion with two verniers presented one after the other at the same location. When the offsets are in the same direction, performance improves. When the offsets are in opposite direction, they cancel each other out. Sequential metacontrast therefore shows that features are integrated across different retinotopic locations. Integration is almost linear (Otto et al., 2006, 2008). We propose that the first vernier and all flankers are interpreted as being part of a whole (the motion of one line) and, for this reason, the individual elements are rendered invisible. Similar feature inheritance like effects, called feature transposition or feature attribution[2], have been reported also in other paradigms (Werner, 1935; Stewart and Purcell, 1970; Wilson and Johnson, 1985; Hofer et al., 1989; Herzog and Koch, 2001; Parkes et al., 2001; Enns, 2002; Nishida et al., 2005; Öğmen et al., 2006; Otto et al., 2006, 2008).

In the sequential metacontrast paradigm the target itself is completely rendered unconscious (direct measure), i.e., observers cannot even tell whether or not there is a vernier. In most other masking paradigms this is not the case, as mentioned above. In these paradigms, even though the target is subjectively invisible, there are still some motion and luminance cues allowing for target detection. As in feature fusion, we have shown that the unconscious vernier changes the perception of a second direct measure, namely the inherited vernier offsets, visible at the flanks. Hence, our paradigm shows unconscious processing that is independent of pre-activations of the motor-cortex, as in masked priming (e.g., Eimer and Schlaghecken, 2000). The invisible vernier target offset is even integrated with offsets of flanking elements, which can be presented more than 400 ms after target onset, which is much longer than the reaction times in mask priming experiments. We have recently shown that feature fusion even precedes motor-priming (Grainger et al., 2013). As in the TMS experiment above, the sequential metacontrast paradigm shows that features of invisible elements can persist in the human brain for substantially long times.

As in the case of vernier fusion at one retinotopic location, non-retinotopic integration follows "flexible" grouping rules as demonstrated in **Figure 3B**. As before, we propose that the human brain first carefully analyzes complex motion trajectories and, then, integrates features along motion streams. Changes in grouping lead to changes in integration.

Such a mechanism makes sense from an ecological perspective. At night, a car is running through a modestly illuminated street. The luminance (color of car ⋆ light shining on car) changes strongly from instance to instance because of the distance between street lights, shadows, reflections, etc. In addition, each

---

[2] These terms emphasize different aspects of the phenomenon. Feature inheritance emphasizes the changes occurring to the mask, feature transposition emphasizes the transfer of the feature from the target to the mask, while feature attribution emphasizes the interpretive process where the target and mask are linked to each other via motion grouping and thus share their features.

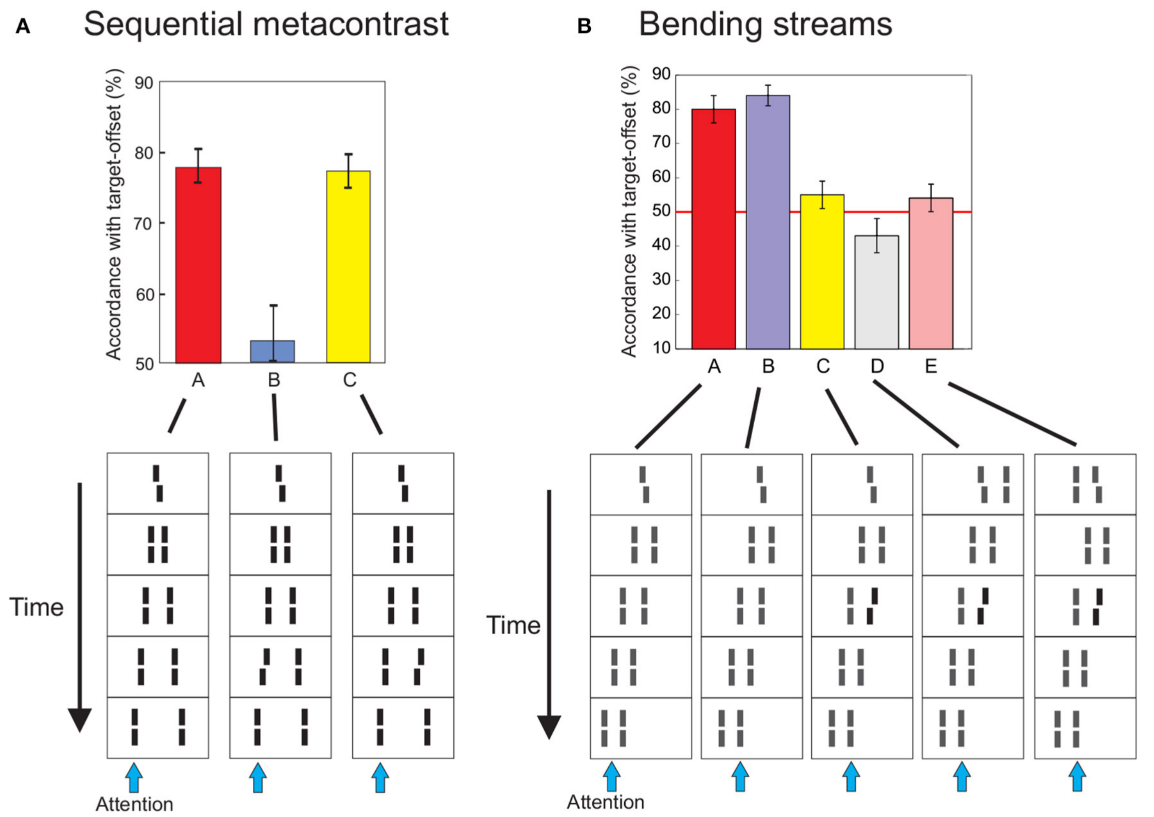


FIGURE 3 | (A) Feature integration also occurs when elements are presented at different retinotopic locations. A central vernier, offset either to the left or right, was flanked by *aligned* verniers after short ISIs leading to the percept of an expanding motion stream. Even though the vernier is invisible by metacontrast masking, its offset is perceived at the aligned verniers. To give quantitative expression, we asked observers to attend to the left (or right) motion stream and report the perceived offset. The task is natural to the observers since the vernier offset is inherited to the flanking lines and thus clearly visible. Adding an opposite offset (anti-offset) to one flanking line, leads to integration as in feature fusion. Integration of vernier and flanker offsets occurs only in the attended stream (blue arrows indicate the attended stream). When the offset of the flanker is presented in the non-attended stream, it is not integrated with the vernier offset (C). **(B)** Integration depends on flexible grouping. We presented "bending streams" leading to similar integration of the vernier offset when observers attend to either the right or left stream because the vernier is inherited to both streams (A,B). In (C) we added an anti-offset to the second flanker of the right stream, i.e., at the same spatial location as the central vernier. The vernier and flanker offset integrated. Next, we added single lines to the vernier, which changed the spatio-temporal grouping and, accordingly, feature integration (D, E). If the line is presented to the left of the vernier, the vernier is inherited to the left stream only and hence its offset is integrated in the left stream. For this reason, the vernier offset is not integrated in the right stream and thus the flanker anti-offset dominates performance when observers attend to the right stream (performance is below 50% because the flanker offset is always offset in the opposite direction than the vernier). (E) When the single line in the first frame is placed to the left of the central vernier, grouping and hence performance changes. The vernier offset is now exclusively integrated in the right stream and thus vernier and flanker offset cancel each other. Figures adopted from Otto et al. (2006).

photoreceptor receives information only for a very short time. Hence, averaging across the motion trajectory is a first step to compute the "true" color of the car, independent of the illumination. In addition, the car may disappear when passing through a shadow. During this period, averaging needs to stop and only continue when the car reappears. Similarly, we have shown that the brain stores vernier offset information in a short term memory when the verniers are occluded. After re-appearance the memory re-opens and continues averaging vernier offsets (Scharnowski et al., 2007b).

3. DISCUSSION

3.1. INVISIBILITY UNDER DIFFERENT MASKING TYPES

How a visible stimulus becomes invisible due to the presence of another stimulus is the focus of visual masking research (Bachmann, 1994; Breitmeyer and Öğmen, 2006). Visual masking is not a unitary phenomenon and several different types of masking have been identified. First, one can classify masking into two broad types, masking by light and masking by pattern (Breitmeyer and Öğmen, 2006). In masking by light, the mask consists of a uniform light field. The loss of target visibility in this masking type can be explained by the aforementioned low-level irreversible factors related to dynamic range adjustments. Masking by pattern can be divided into two broad types, pattern masking by noise and pattern masking by structure (Breitmeyer and Öğmen, 2006). In pattern masking by noise, the mask is a noise pattern, such as an array of randomly placed dots, which do not bear structural similarity to the target. Here, with appropriate timing, the target and mask integrate into one conglomerate thereby hampering the visibility of the target (Breitmeyer and Öğmen, 2006).

However, we claim that a different process takes place when both the target and mask have structure and the visual system forms Gestalts both in space and time (Ternus, 1938). We suggest that this process is flexible in that it can lead to integration or segregation in time depending on the context. Thus, invisibility arising from temporal integration is not a limitation of visual system due to its slow dynamics, but rather a purposeful computation as part of selecting the best Gestalt across space and time.

More recently, it has been proposed that four-dot masking, also known as object substitution masking or common onset masking, is a fundamentally different type of masking (Enns and Di Lollo, 1997, 2000; Di Lollo et al., 2000). Even though there is a debate whether this is a truly different type of masking (Breitmeyer and Öğmen, 2000; Di Lollo et al., 2002; Francis and Hermens, 2002; Breitmeyer and Öğmen, 2006) it is important to highlight some similarities and differences between two models that are based on this paradigm and our approach. These accounts, known as object substitution or updating masking, are based on object-level representations (Enns and Di Lollo, 1997, 2000; Di Lollo et al., 2000; Lleras and Moore, 2003; Moore and Lleras, 2005; Pilling and Gellatly, 2010). They propose that the invisibility of a target results from the substitution or updating of the target representation by the mask representation during the iterative activities set up in cortical reentrant (feedback) loops. Under the four-dot or common onset masking conditions, the features of the invisible target are incorporated into the mask. Thus, according to these theories, feature attribution is clearly linked to the process of masking by the common process of object substitution, which occurs during reentrant object updating[3]. Hence, these approaches predict a strong correlation between feature attribution and masking. On the other hand, in our approach we predict a dissociation between visual masking and feature attribution (Öğmen, 2007; Öğmen and Herzog, 2010; Öğmen et al., 2006; Otto et al., 2006; Noory et al., under review). We tested these contrasting predictions in a study where we determined the correlations between feature attribution, masking, and motion (Breitmeyer et al., 2008). We found that feature attribution correlated strongly with motion, but not with backward masking (Breitmeyer et al., 2008). Thus, these results argue against object substitution or updating models and support a model wherein feature attribution and masking serve complementary but distinct roles (Öğmen, 2007; Öğmen and Herzog, 2010).

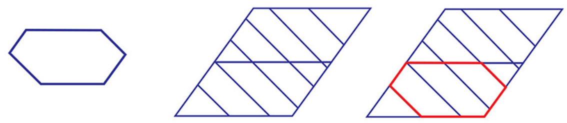
3.2. THE MANY MECHANISMS OF INVISIBILITY

Invisibility, as a goal and interpretation, is ubiquitous, occurs on many levels wherever the human brain needs to solve the ill-posed problems of vision (see below). For example, the hexagon on the left of **Figure 4A** is clearly visible. The shape in the middle contains this hexagon as well, but due to the grouping of the oblique lines into a global but simpler pattern, the hexagon becomes invisible. Highlighting the hexagon by a color difference leads to another perceptual organization where the hexagon becomes visible again. Other well known examples are binocular rivalry and ambiguous figures (**Figure 4**). There are many other "flexible" mechanisms that can render a target invisible. For example in change blindness, a target, even though presented for extended amounts of time, is invisible because of a lack of attention (for reviews, see Simons and Rensink, 2005; Simons and Levin, 1997). Moreover, it has been shown that visibility of the target in masking is influenced by the task. In particular, differences are found when participants are asked to report the luminance of the target, compared to when they are asked to respond as quickly as possible to the location of the target (Fehrer and Raab, 1962; Schiller and Smith, 1966; Öğmen et al., 2003). Hence, visibility of the brightness of a stimulus may be impaired in different ways than the visibility of the spatial position of a stimulus, because the two aspects of the stimuli may be represented differently (Breitmeyer and Öğmen, 2006).

However, we do not claim that invisibility is always interpretation. To the contrary, as mentioned above, low level limitations can render a target irreversibly invisible, for example, when the mask is of high luminance.

So far, we have considered grouping from a Gestalt psychology point of view. At the moment, we do not want to speculate on

A Invisibility by grouping



B Face-vase illusion

C Ill-posed problem of shape

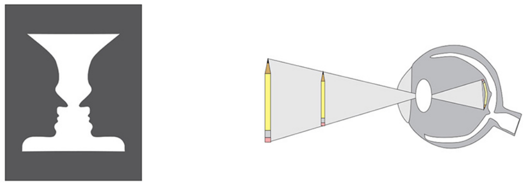


FIGURE 4 | (A) The hexagon on the left is clearly visible. The very same hexagon is hard to find in the shape in the middle because adding further elements leads to a very different perceptual organization. A simpler overall shape is perceived and the hexagon, as a sub-shape, is rendered invisible (solution on the right, shape in red). Adopted from Aydin et al. (2011). **(B)** Either a face or a vase is perceived. It is impossible to see both interpretations at the same time (Rubin, 1915). **(C)** The retina codes the external world by a 2-D representation. Hence, the brain needs to infer the third dimension. For example, there are infinitely many pens (only two are shown) that give rise to the same retinal image. To infer which pen is presented, the human brain needs to estimate two unknowns, namely the size and distance of the pen. This is an ill-posed problem, i.e., there is no unique mathematical solution, since only one value is available, namely the retinal size of the projection of the pen.

---

[3] It is important to note that under four dot masking paradigm, no masking occurs when attention is not divided and directed to the target. From this point of view, object substitution is not applicable to the results shown here because in the presently discussed work the target location is predictable and receives full attentional resources. The object updating account may be applicable depending on specific mechanisms of object updating, which, unfortunately, remain unspecified.

the neural mechanism that underlie interpretation and grouping but just like to mention that more and more neurophysiological evidence (Roelfsema and Houtkamp, 2011; Wannig et al., 2011) is becoming available.

3.3. WHY DOES INVISIBILITY OCCUR AT ALL? WHY IS VISIBILITY UNIQUE AND NOT BAYESIAN?

The idea of invisibility as a goal and interpretation can be traced back to the Gestaltists who forcefully demonstrated that our perceptual experience is *not* a simple collection of stimulus elements but instead is based on the formation of wholes (Gestalts). The visual input consists of a staggering amount of elementary stimulations (the pixels of an image or photo-receptor activations). Because there are "infinitely" many possible ways these stimulations can combine together, "laws" such as proximity, similarity, and good continuation were introduced to limit the number of possible solutions. Guided by classical physics, according to which the state of the world is both unique and determined by a minimum energy principle, the Gestaltists formulated the law of Prägnanz, which states that only the "simplest" solution becomes visible and all other solutions remain invisible (Koffka, 1935).

When different solutions are of *similar* simplicity as in binocular rivalry or ambiguous figures, such as Rubin's face/vase example, a small difference, such as the locus of attention, can cause switches between the prevailing solutions. Nevertheless, still only one solution is visible at a moment (**Figure 4B**).

Why is there only one interpretation at one moment of time? There are infinitely many pens that give rise to the very same retinal image in **Figure 4C**. Hence, there are infinitely many interpretations. This is the classic ill-posed problem of size perception, which is just one example of the many ill-posed problems of vision. Hence, for a unique percept, infinitely many interpretations of one retinal image need to be invisible. For this reason, in ambiguous figures and binocular rivalry, there are not two, but infinitely, many rivaling interpretations, of which only two or a few *can* become visible. Hence, rendering information invisible is a normal feat of the human brain. We like to argue that (in)visibility in masking paradigms often occurs for the same (normal) reasons.

From a philosophical and computational point of view, one may ask why is it that the brain has to select only one of the many possible interpretations for our phenomenal experience. An alternative view would be a Bayesian type of approach where all alternative interpretations become visible with some indication of their likelihood. As mentioned, the Gestalt psychologists were inspired by classical physics and incorporated into their law of Prägnanz the notion that the state of the world is *unique* and is determined by a minimum energy state (Koffka, 1935). We would like to add the following arguments: First, even for stimuli as in the pen example of **Figure 4C**, there are infinite or close to infinite possible interpretations and therefore making all of them visible is not feasible. One may argue that, perhaps one can pick the top *n* most likely interpretations and make this smaller subset visible. Even if we were to pick a small subset at a given time, the combinations across time would still grow toward infinity. Let's assume that a selection is made also in time so as to always limit the number of visible percepts to *n*. The problem with this is that it will break down the unity of consciousness in that the subject will be living in "parallel realities" where different combinations in different percepts can lead to different learning and experiences, whose number and diversity can grow rapidly over time. Thus, we suggest that a unique visible configuration is chosen to maintain the unity of consciousness.

3.4. THE ROLE OF VOLITIONAL CONTROL

We do not claim that interpretation is under the control of volition. To the contrary, integration within the motion streams of the sequential metacontrast paradigm is mandatory (Herzog, 2007). Observers can only choose to which stream they want to attend to but they cannot attend to one line individually (see also Otto et al., 2006, 2008). In addition, integrated features are usually metamers, i.e., it is impossible to judge whether a perceived vernier offset comes from one or several verniers (Herzog and Koch, 2001; Scharnowski et al., 2009; Hermens et al., 2010). The same mechanisms of attention can explain why masking can be influenced by the task (for a discussion, see Breitmeyer and Öğmen, 2006) and individual differences (e.g., Albrecht et al., 2010).

Neither do we claim that invisibility by interpretation does not occur stereotypically. The very same stimulus, presented over and over again, can lead to the very same percept depending on the rules of grouping of visual scenes. In addition, a stimulus may lead to the very same percept for different observers and is thus less variable than, for example, the interpretations of poems.

3.5. METHODOLOGICAL AND CONCEPTUAL IMPLICATIONS FOR (UN)CONSCIOUSNESS RESEARCH

Our results have strong methodological implications for (un)consciousness research. For example, observers cannot report the offset direction of the central vernier in the sequential metacontrast paradigm (**Figure 3**), simply because the vernier is invisible. Still, the offset is, unexpectedly from a retinotopic point of view, visible at the non-offset flanking lines. Hence, visibility may go unnoticed depending on the task of the observers. In fact, in the early reports such feature inheritance like effects were considered as nuisances and potential sources of artifacts of metacontrast masking (see Hofer et al., 1989; Stewart and Purcell, 1970). This is important for unconsciousness research, where the difference in the indirect measure between conscious and unconscious conditions is often rather small in the range of a few milliseconds of reaction times (Naccache et al., 2002). It hence may be possible that observers base their indirect measure decisions on inherited features, but not for the direct measure. In this sense our paradigms offers an interesting alternative to the classic direct-indirect measures by determining unconsciousness with two direct measures, which in addition both measure accuracy in a similar way and have similar sensitivity.

Our results challenge many models of consciousness. For example, invisibility is often proposed to occur because of a lack of recurrent processing (Lamme and Roelfsema, 2000; Dehaene et al., 2001; Naccache et al., 2002). However, in the sequential metacontrast paradigm flankers integrate with the vernier even when presented 300 ms after vernier onset implicating recurrent processing because of the long difference in presentation times and the integration process. In addition, the vernier offset is visible at the flankers and hence needs to be processed by recurrent processing. However, why is then the vernier itself not visible? Why is the vernier spared from recurrent processing but not its offset? These kinds of observations are only possible, because we used direct measures, which allow us to test for long term effects of invisible features. This is impossible with an indirect measure such as speeded reactions times.

4. SUMMARY

We have shown that the visibility of an element can crucially depend on how it is grouped with other elements, even in situations, which were previously attributed to lower limitations. In these cases, we propose that the human brain carefully registers the features of all incoming elements. As our TMS experiments have shown, these features can be stored for a substantial time of more than 400 ms. During this period, the brain collects information to compute which elements belong together and then integrates features into a coherent percept. Visibility and invisibility are just outcomes of this process. Hence, we have argued that much of the invisibility found in perception can be the result of purposeful selections made by the brain. However, there are many other aspects, including low level limitations and attentional selection, which are as crucial for visibility. Hence, it is important to clarify in each paradigm and situation to which extent each of these factors are in operation.

ACKNOWLEDGMENTS

This work was supported by the Swiss National Science Foundation (SNF) project "Basics of visual processing: from retinotopic encoding to non-retinotopic representations."

REFERENCES

Albrecht, T., Klapotke, S., and Mattler, U. (2010). Individual differences in metacontrast masking are enhanced by perceptual learning. *Conscious. Cogn.* 19, 656–666. doi: 10.1016/j.concog.2009.12.002

Aydin, M., Herzog, M. H., and Öğmen, H. (2011). Attention modulates spatio-temporal grouping. *Vision Res.* 51, 435–446. doi: 10.1016/j.visres.2010.12.013

Bachmann, T. (1994). *Psychophysiology of Visual Masking: the Fine Structure of Conscious Experience.* Nova Science.

Breitmeyer, B., and Öğmen, H. (2006). *Visual Masking: Time Slices Through Conscious and Unconscious Vision*, Vol. 41. Oxford: Oxford University Press.

Breitmeyer, B. G., Herzog, M. H., and Öğmen, H. (2008). Motion, not masking, provides the medium for feature attribution. *Psychol. Sci.* 19, 823–829. doi: 10.1111/j.1467-9280.2008.02163.x

Breitmeyer, B. G., and Öğmen, H. (2000). Recent models and findings in visual backward masking: a comparison, review, and update. *Percept. Psychophys.* 62, 1572–1595. doi: 10.3758/BF03212157

Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J.-F., Poline, J.-B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nat. Neurosci.* 4, 752–758. doi: 10.1038/89551

Di Lollo, V. (1980). Temporal integration in visual memory. *J. Exp. Psychol. Gen.* 109:75. doi: 10.1037/0096-3445.109.1.75

Di Lollo, V., Enns, J. T., and Rensink, R. A. (2000). Competition for consciousness among visual events: the psychophysics of reentrant visual processes. *J. Exp. Psychol. Gen.* 129:481. doi: 10.1037/0096-3445.129.4.481

Di Lollo, V., Enns, J. T., and Rensink, R. A. (2002). Object substitution without reentry? *J. Exp. Psychol. Gen.* 131, 594–596. doi: 10.1037/0096-3445.131.4.594

Efron, R. (1967). The duration of the present. *Ann. N.Y. Acad. Sci.* 138, 713–729. doi: 10.1111/j.1749-6632.1967.tb55017.x

Efron, R. (1973). Conservation of temporal information by perceptual systems. *Percept. Psychophys.* 14, 518–530. doi: 10.3758/BF03211193

Eimer, M., and Schlaghecken, F. (2003). Response facilitation and inhibition in subliminal priming. *Biol. Psychol.* 64, 7–26. doi: 10.1016/S0301-0511(03)00100-5

Enns, J. T. (2002). Visual binding in the standing wave illusion. *Psychon. Bull. Rev.* 9, 489–496. doi: 10.3758/BF03196304

Enns, J. T., and Di Lollo, V. (1997). Object substitution: a new form of masking in unattended visual locations. *Psychol. Sci.* 8, 135–139. doi: 10.1111/j.1467-9280.1997.tb00696.x

Enns, J. T., and Di Lollo, V. (2000). What's new in visual masking? *Trends Cogn. Sci.* 4, 345–352. doi: 10.1016/S1364-6613(00)01520-5

Fehrer, E., and Raab, D. (1962). Reaction time to stimuli masked by metacontrast. *J. Exp. Psychol.* 63, 143. doi: 10.1037/h0040795

Francis, G., and Hermens, F. (2002). Comment on "competition for consciousness among visual events: the psychophysics of reentrant visual processes"(di lollo, enns & rensink, 2000). *J. Exp. Psychol. Gen.* 131, 590–593. doi: 10.1037/0096-3445.131.4.590

Ghose, T., Hermens, F., and Herzog, M. (2013). How the global layout of the mask influences masking strength. *J. Vis.* 13, 826–826. doi: 10.1167/13.9.826

Grainger, J. E., Scharnowski, F., Schmidt, T., and Herzog, M. H. (2013). Two primes priming: does feature integration occur before response activation? *J. Vis.* 13:19. doi: 10.1167/13.8.19

Hermens, F., Scharnowski, F., and Herzog, M. H. (2009). Spatial grouping determines temporal integration. *J. Exp. Psychol. Hum. Percept. Perform.* 35, 595. doi: 10.1037/a0013706

Hermens, F., Scharnowski, F., and Herzog, M. H. (2010). Automatic grouping of regular structures. *J. Vis.* 10, 1–16. doi: 10.1167/10.8.5

Herzog, M. H. (2007). Spatial processing and visual backward masking. *Adv. Cogn. Psychol.* 3, 85–92. doi: 10.2478/v10053-008-0016-1

Herzog, M. H., and Fahle, M. (2002). Effects of grouping in contextual modulation. *Nature* 415, 433–436. doi: 10.1038/415433a

Herzog, M. H., and Koch, C. (2001). Seeing properties of an invisible object: feature inheritance and shine-through. *Proc. Natl. Acad. Sci. U.S.A.* 98, 4271–4275. doi: 10.1073/pnas.071047498

Herzog, M. H., Parish, L., Koch, C., and Fahle, M. (2003). Fusion of competing features is not serial. *Vision Res.* 43, 1951–1960. doi: 10.1016/S0042-6989(03)00278-5

Hofer, D., Walder, F., and Gronër, M. (1989). Metakontrast: ein berühmtes, aber schwer messbares phänomen. *Schweizerische Zeitschrift für Psychologie und ihre Anwendungen* 48, 219–232.

Kahneman, D. (1968). Method, findings, and theory in studies of visual masking. *Psychol. Bull.* 70, 404. doi: 10.1037/h0026731

Klotz, W., and Neumann, O. (1999). Motor activation without conscious discrimination in metacontrast masking. *J. Exp. Psychol. Hum. Percept. Perform.* 25:976. doi: 10.1037/0096-1523.25.4.976

Koffka, K. (1935). *Principles of Gestalt Psychology*. New York, NY: Harcourt, Brace.

Lamme, V. A., and Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* 23, 571–579. doi: 10.1016/S0166-2236(00)01657-X

Lleras, A., and Moore, C. M. (2003). When the target becomes the mask: using apparent motion to isolate the object-level component of object substitution masking. *J. Exp. Psychol. Hum. Percept. Perform.* 29:106. doi: 10.1037/0096-1523.29.1.106

Moore, C. M., and Lleras, A. (2005). On the role of object representations in substitution masking. *J. Exp. Psychol. Hum. Percept. Perform.* 31, 1171. doi: 10.1037/0096-1523.31.6.1171

Naccache, L., Blandin, E., and Dehaene, S. (2002). Unconscious masked priming depends on temporal attention. *Psychol. Sci.* 13, 416–424. doi: 10.1111/1467-9280.00474

Nishida, S., Watanabe, J., and Kuriki, I. (2005). Motion-induced colour segregation. *J. Vis.* 5, 279–279. doi: 10.1167/5.8.279

Öğmen, H. (2007). A theory of moving form perception: synergy between masking, perceptual grouping, and motion computation in retinotopic and non-retinotopic representations. *Adv. Cogn. Psychol.* 3, 67. doi: 10.2478/v10053-008-0015-2

Öğmen, H., Breitmeyer, B. G., and Melvin, R. (2003). The what and where in visual masking. *Vision Res.* 43, 1337–1350. doi: 10.1016/S0042-6989(03)00138-X

Öğmen, H., and Herzog, M. H. (2010). The geometry of visual perception: retinotopic and nonretinotopic representations in the human visual system. *Proc. IEEE* 98, 479–492. doi: 10.1109/JPROC.2009.2039028

Öğmen, H., Otto, T. U., and Herzog, M. H. (2006). Perceptual grouping induces non-retinotopic feature attribution in human vision. *Vision Res.* 46, 3234–3242. doi: 10.1016/j.visres.2006.04.007

Otto, T. U., Öğmen, H., and Herzog, M. H. (2006). The flight path of the phoenix: the visible trace of invisible elements in human vision. *J. Vis.* 6, 1079–1078. doi: 10.1167/6.10.7

Otto, T. U., Öğmen, H., and Herzog, M. H. (2008). Assessing the microstructure of motion correspondences with non-retinotopic feature attribution. *J. Vis.* 8, 1–15. doi: 10.1167/8.7.16

Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., and Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nat. Neurosci.* 4, 739–744. doi: 10.1038/89532

Pilling, M., and Gellatly, A. (2010). Object substitution masking and the object updating hypothesis. *Psychon. Bull. Rev.* 17, 737–742. doi: 10.3758/PBR.17.5.737

Pilz, K. S., Zimmermann, C., Scholz, J., and Herzog, M. H. (2013). Long-lasting visual integration of form, motion, and color as revealed by visual masking. *J. Vis.* 13, 1–11. doi: 10.1167/13.10.12

Roelfsema, P. R., and Houtkamp, R. (2011). Incremental grouping of image elements in vision. *Attent. Percept. Psychophys.* 73, 2542–2572. doi: 10.3758/s13414-011-0200-0

Rubin, E. (1915). *Visuell Wahrgenommene Figuren*. Copenhagen: Gyldendalske Boghandel.

Scharnowski, F., Hermens, F., and Herzog, M. H. (2007a). Bloch's law and the dynamics of feature fusion. *Vision Res.* 47, 2444–2452. doi: 10.1016/j.visres.2007.05.004

Scharnowski, F., Hermens, F., Kammer, T., Öğmen, H., and Herzog, M. H. (2007b). Feature fusion reveals slow and fast visual memories. *J. Cogn. Neurosci.* 19, 632–641. doi: 10.1162/jocn.2007.19.4.632

Scharnowski, F., Rüter, J., Jolij, J., Hermens, F., Kammer, T., and Herzog, M. H. (2009). Long-lasting modulation of feature integration by transcranial magnetic stimulation. *J. Vis.* 9, 1–10. doi: 10.1167/9.6.1

Scheerer, E. (1973). Integration, interruption and processing rate in visual backward masking. *Psychol. Forsch.* 36, 71–93. doi: 10.1007/BF00424655

Schiller, P. H., and Smith, M. C. (1966). Detection in metacontrast. *J. Exp. Psychol.* 71:32. doi: 10.1037/h0022617

Schmidt, T. (2002). The finger in flight: real-time motor control by visually masked color stimuli. *Psychol. Sci.* 13, 112–118. doi: 10.1111/1467-9280.00421

Sharikadze, M., Fahle, M., and Herzog, M. H. (2005). Attention and feature integration in the feature inheritance effect. *Vision Res.* 45, 2608–2619. doi: 10.1016/j.visres.2005.03.021

Simons, D. J., and Levin, D. T. (1997). Change blindness. *Trends Cogn. Sci.* 1, 261–267. doi: 10.1016/S1364-6613(97)01080-2

Simons, D. J., and Rensink, R. A. (2005). Change blindness: past, present, and future. *Trends Cogn. Sci.* 9, 16–20. doi: 10.1016/j.tics.2004.11.006

Stewart, A. L., and Purcell, D. G. (1970). U-shaped masking functions in visual backward masking: effects of target configuration and retinal position. *Percept. Psychophys.* 7, 253–256. doi: 10.3758/BF03209373

Ternus, J. (1938). *The Problem of Phenomenal Identity.* London: Kegan Paul, Trench, Trubner and Company.

Turvey, M. T. (1973). On peripheral and central processes in vision: inferences from an information-processing analysis of masking with patterned stimuli. *Psychol. Rev.* 80:1. doi: 10.1037/h0033872

Vorberg, D., Mattler, U., Heinecke, A., Schmidt, T., and Schwarzbach, J. (2003). Different time courses for visual perception and action priming. *Proc. Natl. Acad. Sci. U.S.A.* 100, 6275–6280. doi: 10.1073/pnas.0931489100

Wannig, A., Stanisor, L., and Roelfsema, P. R. (2011). Automatic spread of attentional response modulation along gestalt criteria in primary visual cortex. *Nat. Neurosci.* 14, 1243–1244. doi: 10.1038/nn.2910

Werner, H. (1935). Studies on contour: I. qualitative analyses. *Am. J. Psychol.* 47, 40–64. doi: 10.2307/1416707

Wilson, A. E., and Johnson, R. M. (1985). Transposition in backward masking the case of the travelling gap. *Vision Res.* 25, 283–288. doi: 10.1016/0042-6989(85)90120-8

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 06 March 2014; accepted: 18 August 2014; published online: 17 September 2014.

Citation: Herzog MH, Hermens F and Öğmen H (2014) Invisibility and interpretation. Front. Psychol. ***5****:975. doi: 10.3389/fpsyg.2014.00975*

This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 23 September 2014
doi: 10.3389/fpsyg.2014.01080

Evidence of weak conscious experiences in the exclusion task

Kristian Sandberg*[1,2]*, ***Simon H. Del Pin*[3]**, ***Bo M. Bibby*[4]** ***and Morten Overgaard*[1,3]**

[1] Cognitive Neuroscience Research Unit – Center of Functionally Integrative Neuroscience, Hammel Neurorehabilitation and Research Centre – Danish Neuroscience Center, Aarhus University Hospital, Aarhus, Denmark
[2] Institute of Cognitive Neuroscience, University College London, London, UK
[3] Department of Communication and Psychology, Center for Cognitive Neuroscience, Aalborg University, Aalborg, Denmark
[4] Department of Biostatistics, Aarhus University, Aarhus, Denmark

Edited by:
Nathan Faivre, California Institute of Technology, USA

Reviewed by:
Zoltan Dienes, University of Sussex, UK
Bert Timmermans, University of Aberdeen, UK

****Correspondence:***
Kristian Sandberg, Cognitive Neuroscience Research Unit – Center of Functionally Integrative Neuroscience, Hammel Neurorehabilitation and Research Centre – Danish Neuroscience Center, Aarhus University Hospital, Nørrebrogade 44, Building 10G, 8000 Aarhus, Denmark
e-mail: krissand@rm.dk

Exclusion tasks have been proposed as objective measures of unconscious perception as they do not depend upon subjective ratings. In exclusion tasks, participants have to complete a task without using a previously presented prime. Use of the prime is taken as evidence for unconscious processing in the absence of awareness, yet it may also simply indicate that participants have weak experiences but fail to realize that these affect the response or fail to counter the effect on the response. Here, we tested this claim by allowing participants to rate their experience of a masked prime on the perceptual awareness scale (PAS) after the exclusion task. Results showed that the prime was used almost as often when participants reported having seen a "weak glimpse" of the prime as when they claimed to have "no experience" of the prime, thus suggesting participants frequently have weak (possibly contentless) experiences of the stimulus when failing to exclude. This indicates that the criteria for report of awareness is lower (i.e., more liberal) than that for exclusion and that failure to exclude should not be taken as evidence of complete absence of awareness.

Keywords: consciousness, exclusion paradigm, perceptual awareness scale, subliminal perception, unconscious processing

INTRODUCTION

Although it is more than a 100 years since Sidis (1898) used subjective measures of visual perception, the last decade has brought about an increased scientific interest in the topic. The main question in this line of research is how conscious experience is optimally measured behaviorally. One popular method is to examine the relationship between the accuracy with which some task is performed and indications from a measure of awareness.

The measure of awareness can be relatively direct and openly subjective – e.g., asking participants to report their conscious experience (e.g., Ramsøy and Overgaard, 2004; Lau and Passingham, 2006; Overgaard et al., 2006; Rounis et al., 2010). However, conscious information is typically defined as the information that can be used for overt behaviour or higher-order cognition, and some measures utilize this connection. Some measures require participants to judge their confidence in being correct (a higher-order decision; e.g., Dienes et al., 1995), and other measures ask participants to place wagers on the correctness of their reply (a process presumed to be guided by the information available for higher-order cognition; e.g., Persaud et al., 2007). Recently, several studies have been conducted comparing these types of awareness measures as will be shown below.

When comparing different measures of awareness, researchers have used several approaches. One popular method is the "subjective threshold" or "dissociation" approach. Here, participants typically perform a forced-choice detection or discrimination task and subsequently rate their experience of the stimulus. Unconscious processing, in this case, is presumed to be responsible for any above-chance performance found when stimuli are below the so-called subjective criterion (i.e., when participants claim to have no experience of the identity of the stimulus; Snodgrass and Shevrin, 2006).

The ideal subjective measure should detect all relevant conscious knowledge (or all experiences; Merikle, 1982; Reingold and Merikle, 1988, 1990; Merikle and Joordens, 1997). Exhaustiveness, i.e., the degree to which conscious processing is detected (Reingold and Merikle, 1988), has been compared between scales in previous studies. Typically, a scale is considered more exhaustive if it indicates less unconscious processing by the guessing criterion (as explained above) and/or more conscious processing by the zero correlation criterion (a measure of how well awareness ratings predict task accuracy; Dienes et al., 1995; Sandberg et al., 2010). Unfortunately, the problems associated with poor exhaustiveness cannot be solved simply by preferring the scale that shows the greatest sensitivity as some scales misclassify unconscious information as conscious – that is, they are not exclusive (Reingold and Merikle, 1988). Generally, the solution is to compare scales for which there is no *a priori* reason to assume a difference in exclusiveness.

Using this approach, one study found that post-decision wagering (PDW) was generally inferior to confidence ratings (CR) in an artificial grammar paradigm because PDW was affected by loss aversion (Dienes and Seth, 2009). Another study replicated this finding for visual identification, but also found that ratings on the perceptual awareness scale (PAS) were more exhaustive than CR (Sandberg et al., 2010). This finding was replicated in a very recent study (using a gender identification task), but only when awareness ratings were made after the identification task (the study found that most scales indicated less awareness when used before the identification task; Wierzchoń et al., 2014). PAS has also been found to be more exhaustive than dichotomous ratings of awareness (Overgaard et al., 2006). Based on these studies and more, we have previously ventured the hypothesis that the most exhaustive measure may simply be asking participants directly about their experience (Overgaard et al., 2010; Overgaard and Sandberg, 2012), and that especially PDW is best used when participants are unable to use a more direct measure (e.g., in studies with non-human animals; Sandberg et al., 2013). Generally, we tentatively propose that whenever participants report their awareness indirectly, whatever task they perform, it introduces an extra process that might fail, or it requires participants to be able to link the quality of experience with task performance flawlessly.

Nevertheless, examining the relationship between task accuracy and different types of awareness ratings is not the only method for examining unconscious processing, and it may indeed be claimed that the core problem of any subjective rating approach is to rule out weak conscious perception explanations, i.e., that what appears to be subliminal, in fact, is an effect of weak conscious perception (c.f. Snodgrass, 2002). One way to avoid subjective ratings altogether is by using so-called exclusion tasks (Jacoby et al., 1993; Debner and Jacoby, 1994; Jacoby, 1998). Here, participants are asked to solve an experimental task without using information from a briefly presented prime. Participants thus compare their candidate response with the prime (Jacoby, 1998; Visser and Merikle, 1999), and the reasoning is that overt exclusion of the prime is possible as long as it is consciously perceived, but if the prime (or some aspects of it) were perceived unconsciously, it influences performance and produces above-chance relative match frequencies. Although it has recently been argued (Persaud and McLeod, 2014) that the method fulfills all criteria for an optimal measure of awareness as proposed by Newell and Shanks (2014), it is presently an open question how participants rate their awareness when failing to exclude and whether such exclusion approaches less vulnerable to weak conscious perception explanations than PAS. It is imperative for the validity of exclusion tasks that no conscious perception is found when exclusion fails following the assumptions set up by Merikle and Joordens when explaining the meaning of exclusion failure:

> "The fact that the immediately preceding words were used as responses despite the instructions not to use the words suggests that masked words were perceived without awareness, at least on some proportion of the trials. This interpretation follows from two critical assumptions. First, conscious perception of the immediately preceding word leads subjects not to use it to complete the stem. [...] Second, responses are controlled by conscious influences whenever either conscious influences alone or both conscious and unconscious influences are present"
> (Merikle and Joordens, 1997, p. 113).

It is thus stated that conscious perception takes priority so that whenever conscious perception is present, participants exclude successfully, and exclusion failure is thus an indicator of the (complete) absence of awareness. However, if consciousness is graded or continuous, some potential problems occur, namely the problem of the presence of weak conscious perception. In this context, it has been claimed that exclusion tasks share the potential problems of subjective threshold approaches (Snodgrass, 2002; Snodgrass and Shevrin, 2006). The criticism has been formulated from a single-process signal detection theory perspective, but one does not need to accept this view in order to consider or accept the criticism. The main argument behind the criticism is that sensory evidence in general is continuous, and the participant will only exclude the candidate word on a given trial if the evidence exceeds a certain threshold. This necessitates that a criterion is set for when to exclude, and from the single-process signal detection theory perspective there is no guarantee that this criterion reflects anything but a decision with its own criterion. From a less radical perspective, it may simply be argued that the criterion for exclusion is not necessarily the most exhaustive, and it may indeed be possible that participants weak experiences before they exclude, just as they report weak experiences on the PAS before they report them on a dichotomous scale or before they report any confidence in being correct (Overgaard et al., 2006; Sandberg et al., 2010). This is an empirical question, and examining whether participants have weak experiences when they fail to exclude (thus rejecting the second premise of Merikle and Joordens) is possible. This is related to the exhaustiveness of exclusion tasks.

In this context, it should be emphasized that there are several aspects to exhaustiveness. One aspect that we have highlighted above is whether exclusion failure is vulnerable to the weak conscious perception criticism, i.e., whether participants report weak experiences when they fail to exclude, and this aspect is critical for the validity of the use of exclusion tasks in isolation. Another aspect is the general level of metacognition indicated by each measure – i.e., whether awareness ratings or exclusion performance indicate the most unconscious processing. This last question is difficult to answer without using the process dissociation procedure (PDP) to estimate unconscious processing based on both inclusion and exclusion task performance, and this aspect is thus beyond the goal of the present study. The goal here is to examine whether exclusion failure should be accepted as evidence for the complete absence of awareness.

In the present study, we specifically examined the relationship between exclusion failure and awareness ratings by asking participants to perform an exclusion task and subsequently rate their awareness of the prime using the PAS. We hypothesized that if exclusion requires less sensory evidence than reporting weak experiences, above-chance failure to exclude should be observed only for the lowest awareness rating, and awareness ratings are thus likely to be affected to the weak conscious perception criticism (i.e., participants are unwilling/unable to report weak experience that they nevertheless use to guide overt behavior). If, however, above-chance failure to exclude is also observed when participants report some awareness of the prime, participants require less sensory evidence to report weak experiences than to exclude (and the weak perception criticism thus applies to the exclusion task). This would mean that exclusion failure should not be taken as evidence for the complete absence of conscious perception and that the second assumption put forward by Merikle and Joordens (1997) is not true. The result would also generally support the claim that failure to exclude is sometimes a matter of not trusting weak perception enough to use it to exclude or that the weak perception is so poor that it simply cannot be used (we will return to this issue in the Discussion).

MATERIALS AND METHODS

PARTICIPANTS

Sixteen healthy participants (nine females) with normal or corrected-to-normal vision gave informed consent to participate in the experiment. The mean age was 24.9 years (SD = 1.67). The local ethics committee, De Videnskabsetiske Komitéer for Region Midtjylland, provided written confirmation that no ethical approval was required for the study according to Danish law, specifically Komitéloven §7 and §8.1.

APPARATUS AND STIMULI

Stimuli were generated and displayed in Spyder 2.1.11[1] using Python 2.6.6[2] and PsychoPy v.1.74.01[3]. They were displayed on a 14″ LED monitor with a screen resolution of 1366 × 768 at a refresh rate of 60 Hz. Stimuli consisted of 308 four to six letter Danish words, and masks were rows of six pseudorandom letters. Words were found using a Danish frequency dictionary, and it was confirmed that at least two four to six letter words could be constructed using the first three letters of any individual target word.

PROCEDURE

Participants performed an exclusion task in which they were asked to complete a three letter word stem *without* using a briefly displayed primed word (**Figure 1**). The three letter word stem was always identical to the first three letters of the primed word. At the onset of each trial, a fixation mark appeared for 500 ms. The fixation mark was followed by a forward mask consisting of six pseudorandom letters displayed for 50 ms. Next followed the prime word with a duration pseudorandomly selected between 11 possibilities between 0 and 200 ms with no possibilities in the interval between 150 and 200 ms: {0, 16.7,..., 133.3, 150, 200}. For prime durations of 0 ms, no prime was presented. The prime was followed by a backward mask consisting of six pseudorandom letters displayed for 50 ms. A word stem consisting of the first three letters of the target word followed the backward mask and remained on screen until participants had completed the word stem or until 10 s had passed. Finally, a graphical representation of the PAS (**Table 1**) appeared on screen, and participants were asked to indicate their experience of the prime word using the keyboard number keys. The response options were: “1: No experience” (NE), “2: Weak glimpse” (WG), “3: An almost clear experience” (ACE), and “4: A clear experience” (CE). It is important to note that PAS is not simply a “labeled four-point scale” (Sandberg et al., 2013). In some publications using PAS, scale points are discussed as PAS1–PAS4 (e.g., Overgaard et al., 2006; Timmermans et al., 2010), whereas in others, they are discussed as the category labels NE, WG, ACE, CE (e.g., in Overgaard et al., 2008, 2013). Whereas this is just a matter of wording, the latter indicates more directly that PAS crucially depends on the definition of the four categories. Thus, participants were instructed that NE should be used when there is no experience at all, not even a faint sensation. WG should be used when there is a very weak/vague visual experience without any ability to specify what was perceived. ACE should be is used when there is an experience of what was perceived, yet unclear or blurry. CE should be used when there is a clear experience of what is perceived.

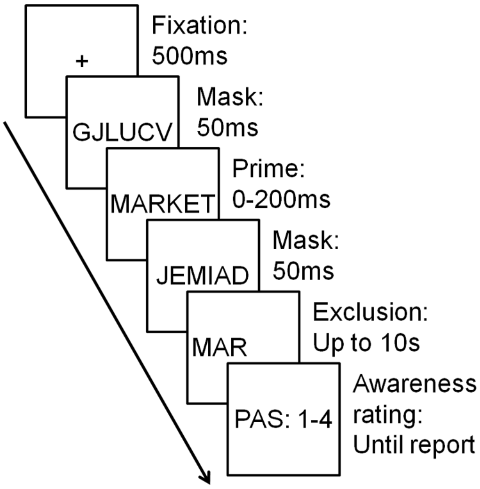


FIGURE 1 | Experimental paradigm. A forward and backward masked prime lasting between 0 and 200 ms was presented on each trial. Following prime presentation, a three letter word stem appeared on screen and participants had to complete the word stem with any word except the prime. In the example shown here, participants should avoid writing “MARKET,” but could write “MARCH” or “MARS” for instance. After this, participants reported their awareness of the prime using the perceptual awareness scale (PAS).

Table 1 | The perceptual awareness scale (PAS).

Label	Description (from Ramsøy and Overgaard, 2004)
(1) No experience	No impression of the stimulus. All answers are seen as mere guesses
(2) A weak experience	A feeling that something has been shown. Not characterised by any content, and this cannot be specified any further
(3) An almost clear experience	Ambiguous experience of the stimulus. Some stimulus aspects are experienced more vividly than others. A feeling of almost being certain about one’s answer
(4) A clear experience	Non-ambiguous experience of the stimulus. No doubt in one’s answer

Scale steps and descriptions.

---

[1] http://code.google.com/p/spyderlib

[2] http://www.python.org

[3] http://www.psychopy.org

The experiment consisted of a practice block and six experimental blocks. For all blocks (including practice), each of the 11 prime durations was used four times in a pseudorandom order, resulting in a total of 44 trials per block. The experiment consisted of 308 trials in total for each participant.

STATISTICAL ANALYSIS

The relationship between awareness ratings and matches of primed and reported words in the exclusion task was analyzed using logistic regression. Match (1 if the prime word was reported within the allotted time-period of 10 s and 0 otherwise) was considered as the dependent variable and awareness rating and stimulus duration along with the interaction between the two as independent variables. A random participant effect was also included in the analysis. Likelihood Ratio (LR) tests were used to assess systematic differences. Data were analysed using Stata version 12.1.

RESULTS

First, the relationship between objective clarity (stimulus duration) and subjective clarity (PAS rating) was examined in order to confirm that different PAS ratings reflected different conscious experiences. As seen in **Figure 2**, mean PAS rating as a function of stimulus duration appeared to have a sigmoidal shape as observed in previous PAS experiments (Sandberg et al., 2011). Furthermore, all PAS ratings were used across a wide range of stimulus durations, but for PAS1 (NE), the mode was 0 ms, for PAS2 (WG) it was 33 ms, for PAS3 (ACE) it was 83 ms, and for PAS4 (CE) it was 200 ms. In other words, when the stimulus became physically clearer, higher PAS ratings were used more frequently, thus indicating that participants used higher PAS ratings to report clearer experiences as instructed.

Next, relative match frequency was plotted for each awareness rating and overall without taking awareness rating into account as a function of stimulus duration (**Figure 3**). In general, above-chance relative match frequencies were observed for PAS1 (NE) and PAS2 (WG; $\chi^2(10) > 98$ and $p < 0.0001$ in both cases) whereas below-chance relative match frequencies were observed for PAS3 (ACE) and PAS4 (CE; $\chi^2(10) > 230$ and $p < 0.0001$ in both cases), with chance defined as the group-level relative match frequency for $t = 0$ ms (12.0%). Significant above-chance relative match frequencies at the $p < 0.05$ level were observed for PAS1 (NE) for all stimulus durations except 17 ms ($p < 0.001$ for all of these except 117 ms). For PAS2 (WG), significant above-chance match were observed for all stimulus durations in the interval 50–133 ms ($p < 0.005$ for 50, 67, and 100 ms). For PAS3 (ACE), significant below-chance relative match frequencies were observed at 17, 100, and 133–150 ms ($p < 0.005$ for 100 ms). For PAS4 (CE), significant below-chance relative match frequencies were observed in the

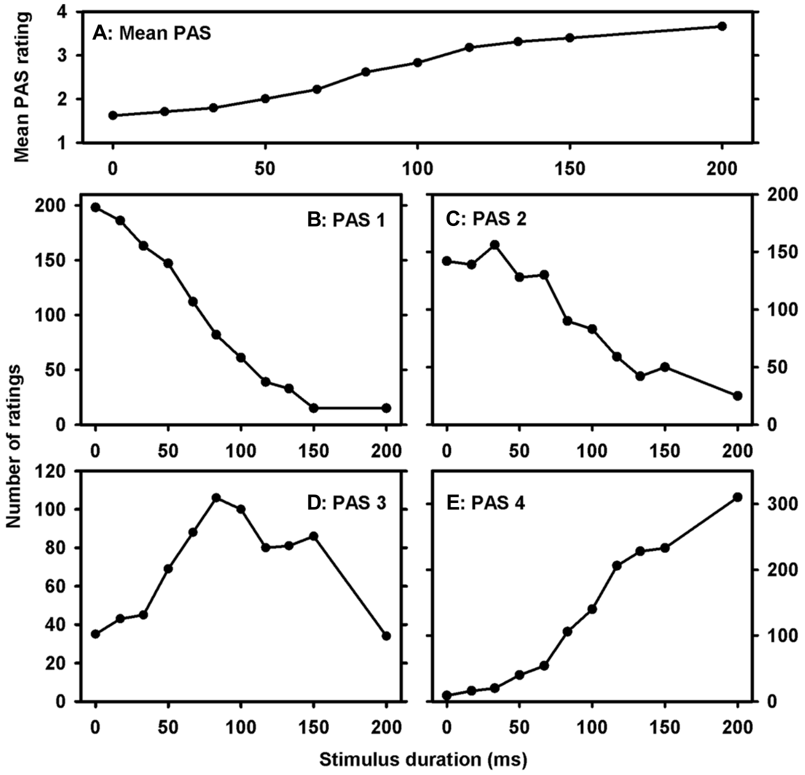


FIGURE 2 | Response distribution. (A) Mean PAS as a function of stimulus duration. **(B–E)** Response distribution as a function of stimulus duration and PAS rating Note that each PAS rating was used across a wide range of stimulus durations and that the mode of each rating was increasing with increasing reported clarity of experience (PAS rating).

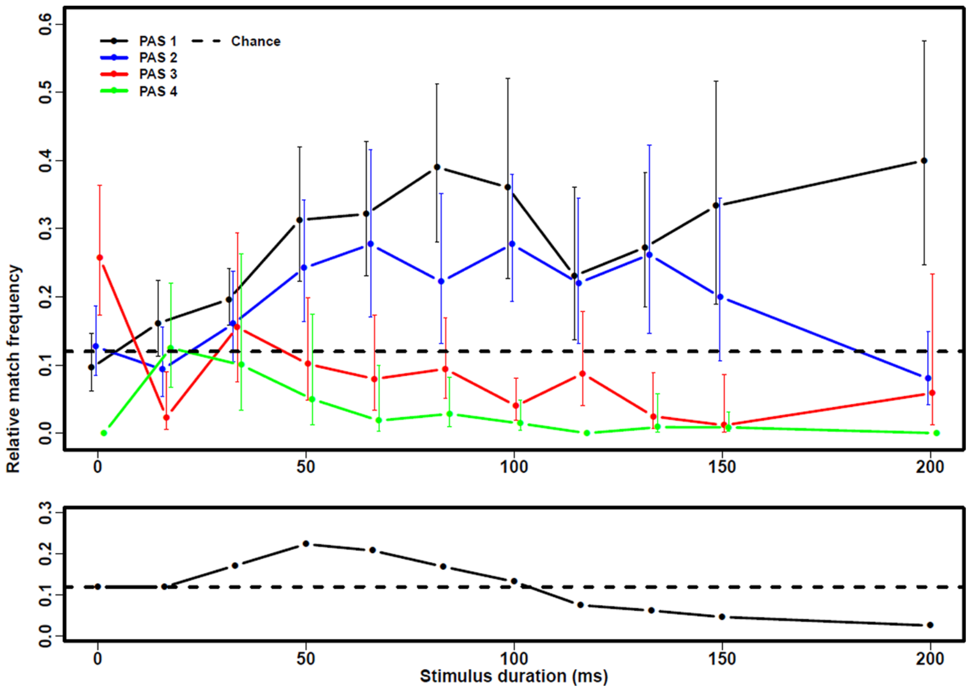


FIGURE 3 | Exclusion performance. (Top) Match frequency (the frequency with which the prime was used to complete the word stem) with 95%-CI from the logistic regression model is plotted as a function of stimulus duration for each PAS rating PAS1 (no experience), PAS2 (a vague experience), PAS3 (an almost clear experience), and PAS4 (a clear experience). At "0 ms", no prime was presented and match frequency here thus reflects the probability of coincidentally selecting the same word as the computer. Note that after around 33 ms, match frequency increases for PAS1-2 and decreases for PAS3-4, indicating that participants fail to exclude both when they report not having seen the prime at all, but also when they had a vague experience of it. **(Bottom)** Overall match frequency as a function of stimulus duration without taking into account PAS rating.

67–200 ms interval ($p < 0.005$ for all of these, except 67 and 133 ms).

Finally, relative match frequency was compared between PAS ratings. A small difference was observed in relative match frequency between PAS1 (NE) and PAS2 (WG; LR $= 21.0 \sim \chi^2(11)$, $p = 0.033$, uncorrected for multiple comparisons). The difference was thus numerically small and not significant if corrections for six comparisons (between all PAS ratings) were made. However, relative match frequencies for both PAS1 (NE) and PAS2 (WG) were statistically significantly higher than for PAS3 (ACE) and PAS4 (CE), and relative match frequencies for PAS4 (CE) were significantly lower than for PAS3 (ACE; LR $> 141.4 \sim \chi^2(11)$ and $p < 0.0001$ for all comparisons).

DISCUSSION

Overall, the results indicated that the criterion for reporting weak experiences was more liberal than the criterion for exclusion, and it is thus unlikely that exclusion tasks are less vulnerable to weak experience critiques than ratings on the PAS. Crucially, this means that exclusion failure should not be taken as evidence of the complete absence of awareness, thus indicating that the second assumption for the validity of exclusion tasks (Merikle and Joordens, 1997) is not true. Specifically, we found that failure to exclude a primed word from report was observed almost to the same extent when participants reported that they had "no experience" of the prime (PAS1) as when they had "a vague experience" or perceived "a weak glimpse" (PAS2), but not when they had "an almost clear experience" (PAS3) or "a clear experience" (PAS4). In other words, participants failed to exclude the prime not only when they claimed to see nothing at all, but also when they had a weak experience of the target. One interpretation is that participants use only highly reliable information to guide overt behavior, yet they are nevertheless consistently able to distinguish weak experiences from the absence of experience.

It appears highly unlikely that the results were caused by PAS ratings being used randomly (i.e., that reports of awareness were unreliable) as it was confirmed that participants used PAS similarly to how it has been used in previous studies, i.e., when the stimulus was physically clearer, higher PAS ratings were used more frequently, thus indicating that participants used higher PAS ratings to report clearer experiences as instructed. These results are consistent with previous observations that PAS ratings do not only increase as a function of physical clarity, but also that each PAS rating is associated with a different accuracy level in stimulus identification (i.e., inclusion) tasks, again indicating that PAS ratings reflect different experiences (Ramsøy and Overgaard, 2004; Sandberg et al., 2010).

For these reasons, it appears more likely that the results were caused by participants being unwilling or unable to let weak (and potentially unreliable) experiences guide exclusion, or that they saw no reason to exclude the first word that came to mind because they were unaware that weak experiences influenced word generation. There are thus at least three interpretations of the results: (1) Participants could have had information that they chose not to use because they did not want to risk indicating confidence in something they were very uncertain about. (2) Participants were unable to use the information that they had. (3) Participants saw no reason to use the information they had as they were unaware that it was reliable.

The first interpretation could be hypothesized as part of the explanation for PAS has fared better than CR in some experiments as participants might fear looking over-confident if they report any confidence in cases where they only have a hunch, but the explanation is not very likely as CR are generally not affected by risk aversion (Dienes and Seth, 2009), and it thus seems unlikely that exclusion tasks should suffer from this. Additionally, in an exclusion task the conservative, risk-averse action might be to exclude even when there is only low confidence in order to avoid reporting something incorrect. This leaves the explanations of inability to use information or simply not using it because it seems irrelevant.

The definition of PAS2 ratings as reflecting subjective detection (but not identification) of a stimulus is relevant to both these interpretations. Specifically, if participants use PAS2 as instructed, they will use it to report that something was presented, but that they do not know what was presented (Ramsøy and Overgaard, 2004). Based on the current experiment, it is nevertheless not possible to distinguish the two interpretations, and we simply conclude that exclusion is typically not performed for weak, possibly contentless experiences. This means that exclusion tasks are unlikely to be a solution to any alternative weak conscious perception accounts that could be used to criticize findings of unconscious perception using the subjective threshold approach with PAS as the criterion for using PAS2 is already very liberal, and more so than for exclusion. Nevertheless, we emphasize that the results of the present experiment should be interpreted with caution as all aspects of exhaustiveness have not been examined. Specifically, it has not been examined if analyses based on PAS ratings indicate less unconscious processing across stimulus durations than the PDP. This comparison is nontrivial and would necessitate that inclusion task performance is also obtained.

Some alternative interpretations should also be discussed. One interpretation of the use of PAS2 ratings – slightly different from the "detection" interpretation – has been proposed by Dienes and Seth (2010). They argue that a given stimulus feature is either perceived or not, and that PAS2 ratings reflect ratings of perceived, but irrelevant, stimulus features. When these irrelevant features are seen, the probability of seeing a relevant feature unconsciously may nevertheless be higher than when nothing is perceived at all, and instead of PAS being more exhaustive than, for instance, CR, it is in fact less exclusive and misclassifies some unconscious information as conscious. This interpretation would also hypothetically account for the findings of the present experiment if PAS2 ratings simply reflect reports about irrelevant information, and that decisions to exclude are based only on all-or-none information about relevant stimulus features. However, the explanation has difficulty accounting for some other observations.

First, if conscious experience were indeed dichotomous, it is difficult to explain why participants consistently claim to perceive images at different levels of clarity, and why different levels of awareness are associated with different levels of task accuracy in identification tasks. A graded/partial awareness perspective (Kouider et al., 2010) can account for this to some extent, but we do not find it convincing in all cases. Graded perception of complex objects is easy to imagine, but it is more difficult when very simple objects, such as line segments only differing in orientation, are used. Here, any graded perception of even a single pixel should be diagnostic and result in peak accuracy, yet this is not observed – accuracy increases slowly as a function of awareness (Overgaard et al., 2006).

Second, if CR (or exclusion decisions) exclusively reflects perception of relevant features whereas PAS reflects perception of both relevant and irrelevant features, it should be expected that whenever ratings of full confidence are given, accuracy should be around peak level and at least as high as for PAS4 ratings (as the participants indicate complete awareness of the relevant features). However, a previous study found that at low stimulus intensities accuracy for PAS4 ratings was very high (almost at 100%) whereas it was relatively poor for CR4 ratings (around 75%, with chance at 25%; Sandberg et al., 2010). The better accuracy-awareness correlation for PAS than for CR is thus not present only for low ratings where weak experiences could lead to subliminal perception. This finding can be explained by CR4 having a lower criterion than PAS4 with all evidence being treated equally, or alternatively that participants are generally worse at using CR [e.g., these ratings reflect a different kind of knowledge (Timmermans et al., 2010)], but PAS ratings reflecting irrelevant information does not explain why participants are not accurate when reporting peak confidence.

These two issues argue against the interpretation that PAS2 ratings simply reflect irrelevant information, and in the context of the present experiment, we thus believe that the evidence weighs in favor of our original accounts. However, even if the alternative account should be true, it does not make PAS use less relevant as participants can generally distinguish these cases of weak (or subliminal) perception from cases of no experience, thus leaving it for the scientist to decide how to treat them in the analyses.

One explanation for a lower criterion for awareness ratings than for exclusion is related to a very recent study (Wierzchoń et al., 2014), which demonstrated that if visual identification is performed before an awareness rating is given, then a higher level of metacognition (i.e., a better relationship between awareness rating and accuracy) is found than when the awareness rating is given before the visual identification task. This may be taken as evidence that performing the visual identification increases metacognition, although it cannot be ruled out entirely that the effect would not be found when simply increasing the time between stimulus presentation and awareness report or when inserting any (i.e., even an unrelated) task. In any case, it could mean that part of the willingness/ability to report weak experiences while failing the exclusion task in the present experiment was caused by the effect of increased metacognition at the time of the awareness report. We do not interpret this as a confound in our study, but rather a potential explanation, as both awareness ratings and the exclusion task were used as they are typically used in the literature; i.e., exclusion tasks are never preceded by awareness ratings, but awareness ratings are almost always preceded by some kind of first order detection or identification task.

In summary, we conclude that participants consistently and reliably report weak experiences when they fail to exclude, thus demonstrating that the second assumption necessary for the validity of exclusion task is not true (the assumption being that whenever there is any conscious perception, even if there is also unconscious perception, participants will exclude). This means that the criterion for reporting weak experiences is more liberal than the criterion for exclusion, and in addition, it is thus unlikely that exclusion tasks are less vulnerable to weak conscious perception explanations than awareness ratings. For these reasons, we argue that there is no evidence in favour of using other methods for acquiring information about participants' experience than allowing them to report it directly – whenever the state of the participants and the experimental context allow for it – and that exclusion failure should not be taken as evidence of absence of awareness. It is more likely to reflect the absence of a certain strength of conscious perception necessary for that perception to be used to guide overt behavior, not a complete absence of awareness. Nevertheless, we emphasize that the present study has not conducted a direct comparison of all aspects of exhaustiveness for awareness ratings and the PDP as a whole. The conclusions thus concern weak experience accounts and the interpretation of exclusion failure, and we encourage direct comparisons of awareness ratings and PDP in future studies.

ACKNOWLEDGMENTS

This work was supported the European Research Council (Kristian Sandberg and Morten Overgaard). We would like to thank Michael Nygaard Pedersen for his help with the making of the experimental program.

REFERENCES

Debner, J. A., and Jacoby, L. L. (1994). Unconscious perception: attention, awareness, and control. *J. Exp. Psychol. Learn. Mem. Cogn.* 20, 304–317. doi: 10.1037/0278-7393.20.2.304

Dienes, Z., Altmann, G. T. M., Kwan, L., and Goode, A. (1995). Unconscious knowledge of artificial grammars is applied strategically. *J. Exp. Psychol. Learn. Mem. Cogn.* 21, 1322–1338. doi: 10.1037/0278-7393.21.5.1322

Dienes, Z., and Seth, A. (2009). Gambling on the unconscious: a comparison of wagering and confidence ratings as measures of awareness in an artificial grammar task. *Conscious. Cogn.* 19, 674–681. doi: 10.1016/j.concog.2009.09.009

Dienes, Z., and Seth, A. K. (2010). Measuring any conscious content versus measuring the relevant conscious content: comment on Sandberg et al. *Conscious. Cogn.* 19, 1079–1080; discussion 1081–1083. doi: 10.1016/j.concog.2010.03.009

Jacoby, L. L. (1998). Invariance in automatic influences of memory: toward a user's guide for the process-dissociation procedure. *J. Exp. Psychol. Learn. Mem. Cogn.* 24, 3–26. doi: 10.1037/0278-7393.24.1.3

Jacoby, L. L., Toth, J., and Yonelinas, A. P. (1993). Separating conscious and unconscious influences of memory: measuring recollection. *J. Exp. Psychol. Gen.* 122, 139–154. doi: 10.1037/0096-3445.122.2.139

Kouider, S., de Gardelle, V., Sackur, J., and Dupoux, E. (2010). How rich is consciousness? The partial awareness hypothesis. *Trends Cogn. Sci.* 14, 301–307. doi: 10.1016/j.tics.2010.04.006

Lau, H. C., and Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 18763–18768. doi: 10.1073/pnas.0607716103

Merikle, P. M. (1982). Unconscious perception revisited. *Percept. Psychophys.* 31, 298–301. doi: 10.3758/BF03202538

Merikle, P. M., and Joordens, S. (1997). "Measuring unconscious influences," in *Scientific Approaches to Consciousness*, eds J. Cohen and J. Schooler (Mahwah, NJ: Erlbaum), 109–123.

Newell, B. R., and Shanks, D. R. (2014). Unconscious influences on decision making: a critical review. *Behav. Brain Sci.* 37, 1–19. doi: 10.1017/S0140525X12003214

Overgaard, M., Fehl, K., Mouridsen, K., Bergholt, B., and Cleeremans, A. (2008). Seeing without seeing? Degraded conscious vision in a blindsight patient. *PLoS ONE* 3:e3028. doi: 10.1371/journal.pone.0003028

Overgaard, M., Lindeløv, J., Svejstrup, S., Døssing, M., Hvid, T., Kauffmann, O., et al. (2013). Is conscious stimulus identification dependent on knowledge of the perceptual modality? Testing the "source misidentification hypothesis." *Front. Psychol.* 4:116. doi: 10.3389/fpsyg.2013.00116

Overgaard, M., Rote, J., Mouridsen, K., and Ramsøy, T. Z. (2006). Is conscious perception gradual or dichotomous? A comparison of report methodologies during a visual task. *Conscious. Cogn.* 15, 700–708. doi: 10.1016/j.concog.2006.04.002

Overgaard, M., and Sandberg, K. (2012). Kinds of access: different methods for report reveal different kinds of metacognitive access. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 367, 1287–1296. doi: 10.1098/rstb.2011.0425

Overgaard, M., Timmermans, B., Sandberg, K., and Cleeremans, A. (2010). Optimizing subjective measures of consciousness. *Conscious. Cogn.* 19, 682–684; discussion 685–686. doi: 10.1016/j.concog.2009.12.018

Persaud, N., and McLeod, P. (2014). Demonstrations of subconscious processing with the binary exclusion task. *Behav. Brain Sci.* 37, 37. doi: 10.1017/S0140525X13000812

Persaud, N., McLeod, P., and Cowey, A. (2007). Post-decision wagering objectively measures awareness. *Nat. Neurosci.* 10, 257–261. doi: 10.1038/nn1840

Ramsøy, T. Z., and Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenol. Cogn. Sci.* 3, 1–23. doi: 10.1023/B:PHEN.0000041900.30172.e8

Reingold, E. M., and Merikle, P. M. (1988). Using direct and indirect measures to study perception without awareness. *Percept. Psychophys.* 44, 563–575. doi: 10.3758/BF03207490

Reingold, E. M., and Merikle, P. M. (1990). On the inter-relatedness of theory and measurement in the study of unconscious processes. *Mind Lang.* 5, 9–28. doi: 10.1111/j.1468-0017.1990.tb00150.x

Rounis, E., Maniscalco, B., Rothwell, J., Passingham, R., and Lau, H. (2010). Theta-burst transcranial magnetic stimulation to the prefrontal cortex impairs metacognitive visual awareness. *Cogn. Neurosci.* 1, 165–175. doi: 10.1080/17588921003632529

Sandberg, K., Bibby, B. M., and Overgaard, M. (2013). Measuring and testing awareness of emotional face expressions. *Conscious. Cogn.* 22, 806–809. doi: 10.1016/j.concog.2013.04.015

Sandberg, K., Bibby, B. M., Timmermans, B., Cleeremans, A., and Overgaard, M. (2011). Measuring consciousness: task accuracy and awareness as sigmoid functions of stimulus duration. *Conscious. Cogn.* 20, 1659–1675. doi: 10.1016/j.concog.2011.09.002

Sandberg, K., Timmermans, B., Overgaard, M., and Cleeremans, A. (2010). Measuring consciousness: is one measure better than the other? *Conscious. Cogn.* 19, 1069–1078. doi: 10.1016/j.concog.2009.12.013

Sidis, B. (1898). *The Psychology of Suggestion*. New York: D. Appleton and Company.

Snodgrass, M. (2002). Disambiguating conscious and unconscious influences: do exclusion paradigms demonstrate unconscious perception? *Am. J. Psychol.* 115, 545–579. doi: 10.2307/1423527

Snodgrass, M., and Shevrin, H. (2006). Unconscious inhibition and facilitation at the objective detection threshold: replicable and qualitatively different unconscious perceptual effects. *Cognition* 101, 43–79. doi: 10.1016/j.cognition.2005.06.006

Timmermans, B., Sandberg, K., Cleeremans, A., and Overgaard, M. (2010). Partial awareness distinguishes between measuring conscious perception and conscious content: reply to Dienes and Seth. *Conscious. Cogn.* 19, 1081–1083. doi: 10.1016/j.concog.2010.05.006

Visser, T. A., and Merikle, P. M. (1999). Conscious and unconscious processes: the effects of motivation. *Conscious. Cogn.* 8, 94–113. doi: 10.1006/ccog.1998.0378

Wierzchoń, M., Paulewicz, B., Asanowicz, D., Timmermans, B., and Cleeremans, A. (2014). Different subjective awareness measures demonstrate the influence of visual identification on perceptual awareness ratings. *Conscious. Cogn.* 27, 109–120. doi: 10.1016/j.concog.2014.04.009

Conflict of Interest Statement: The Review Editor Dr Bert Timmermans declares that, despite having collaborated with authors Dr Kristian Sandberg and Dr Morten Overgaard in the past, the review process was handled objectively and no conflict of interest exists. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 05 March 2014; accepted: 08 September 2014; published online: 23 September 2014.

Citation: Sandberg K, Del Pin SH, Bibby BM and Overgaard M (2014) Evidence of weak conscious experiences in the exclusion task. Front. Psychol. ***5****:1080. doi: 10.3389/fpsyg.2014.01080*

This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 30 July 2014
doi: 10.3389/fpsyg.2014.00804

Waves of visibility: probing the depth of inter-ocular suppression with transient and sustained targets

Lisandro N. Kaunitz[1]*, Alessio Fracasso[2], Māris Skujevskis[3,4] and David Melcher[4,5]

[1] School of Psychological Sciences, Department of Medicine, Nursing and Health Sciences, Monash University, Melbourne, VIC, Australia
[2] Experimental Psychology, Helmholtz Institute, Utrecht University, Utrecht, Netherlands
[3] Cognitive Neuroscience Sector, International School for Advanced Studies, Trieste, Italy
[4] Center for Mind/Brain Sciences (CIMeC), University of Trento, Trento, Italy
[5] Department of Cognitive Sciences, University of Trento, Trento, Italy

Edited by:
Nathan Faivre, California Institute of Technology, USA

Reviewed by:
Zhicheng Lin, University of Washington, USA
Kazushi Maruya, Nippon Telegraph and Telephone Corporation, Japan

***Correspondence:**
Lisandro N. Kaunitz, School of Psychological Sciences, Department of Medicine, Nursing and Health Sciences, Monash University, Room 142, Building 220, 770 Blackburn Road, Clayton, Melbourne, VIC 3168, Australia
e-mail: lisandro.kaunitz@monash.edu.au

In order to study non-conscious visual processing, researchers render otherwise consciously perceived images into invisible stimuli. Through the years, several psychophysical techniques have been developed for this purpose. Yet the comparison of experimental results across techniques remains a difficult task as the depth of suppression depends on the interactions between the type of stimuli and the suppression methods employed. This poses a limit to the inferences that researchers make about the extent of non-conscious processes. We investigated the mechanisms underlying inter-ocular suppression during continuous flash suppression (CFS) and dichoptic visual masking using a transient onset target stimulus and a variety of stimulus/mask temporal manipulations. We show that target duration, timing of target onset, and mask frequency are key aspects of inter-ocular suppression during CFS with transient targets. The differences between our results and sustained target CFS studies suggest that two distinct mechanisms are involved in the detection of transient and prolonged target stimuli during CFS. Our results provide insight into the dynamics of CFS together with evidence for similarities between transient target CFS and dichoptic visual masking.

Keywords: visual awareness, metacognition, continuous flash suppression, masking, vision, binocular, consciousness

INTRODUCTION

The notion that we lack conscious access to most of our brain activity is not new. For decades, researchers have inferred visual non-conscious processes in the brain from subjects' responses to invisible stimuli. What kind of information can the visual system encode without consciousness? The answer to this question depends on the definition of consciousness adopted by researchers and the interaction between the kind of stimuli (e.g., simple lines, images of faces or motion stimuli) and the psychophysical techniques (e.g., inter-ocular suppression, visual crowding, or backward masking) that render those stimuli perceptually invisible (Faivre et al., 2014; Izatt et al., 2014). Different behavioral paradigms achieve stimulus invisibility in different ways and at different levels of neural processing, making the comparison of results among different methods difficult (Kim and Blake, 2005; Fogelson et al., 2014).

Several psychophysical techniques make stimuli invisible via inter-ocular suppression: dissimilar images are presented to the left and right eyes, which leads to the suppression of one of the images from conscious perception. For example, in binocular rivalry (Wheatstone, 1838; Blake and Fox, 1974) two different stimuli are presented each to one eye making the subject's conscious perception alternate between the two. In dichoptic masking (Schiller and Smith, 1968), a mask is shortly presented to one eye immediately before or after a brief target is presented to the other eye. In flash suppression (Wolfe, 1984) a stimulus is initially presented to one eye and after several milliseconds a dissimilar stimulus is presented to the other eye, suppressing the first stimulus for several hundred milliseconds (flash suppression differs from dichoptic masking in that the two stimuli temporally overlap after the onset of the second stimuli). Among these techniques continuous flash suppression (CFS; Tsuchiya and Koch, 2005) constitutes the strongest version, capable of masking stimuli for prolonged periods of time (several seconds). It achieves long periods of suppression with a train of mask patterns (usually referred to as "Mondrians") flashed in rapid succession to one eye while a (typically static) target stimulus is presented to the other eye. CFS has proved a suitable tool for investigating the effects of non-conscious stimuli on, for example, face adaptation (Alais and Melcher, 2007; Stein and Sterzer, 2011), afterimage formation (van Boxtel et al., 2010), and motion processing (Kaunitz et al., 2011, 2013 for a comprehensive review on the scope and limits of non-conscious processing see Lin and He, 2009).

Currently, it is not clear what common mechanisms regulate the balance between visibility and suppression under the various scenarios of dichoptic stimulation. It has been proposed that transient stimuli (of a few tens of milliseconds) under dichoptic visual masking are detected through a "transient channel" triggered by the spatiotemporal edges of the stimulus (Macknik et al., 2000; Breitmeyer and Öğmen, 2006). Target suppression is strongest just before and immediately after a stimulus onset asynchrony (SOA) of 0 ms, suggesting a close relationship between the mask-to-target temporal distance and stimulus visibility. For prolonged presentation of stimuli, it has been reported that CFS exerts its strongest suppression with Mondrians at a frequency of ∼10 Hz (Tsuchiya et al., 2006) but with the exception of this pioneering study, the influence of Mondrian frequency on stimulus suppression has not been investigated systematically.

We conducted four experiments to investigate the dynamics of CFS and the mechanisms of suppression for transient (starting from a few milliseconds) and prolonged (up to several hundred milliseconds) stimuli. The manipulation of the relative temporal distance of presentation between targets and Mondrians allowed us to study the temporal dynamics of stimuli suppression during CFS. Moreover, we investigated the effect of Mondrian frequency and target duration on objective performance and subjective reports of target visibility. We aimed to clarify how the temporal dynamics of CFS determine the depth of suppression for both transient and prolonged stimuli and, in particular, how the timing of the presentation of stimuli within the sequence of Mondrians would affect objective performance, subjective visibility and metacognition—an objective unbiased measure of subjects' awareness of their own responses.

MATERIALS AND METHODS

SUBJECTS

Three authors and 29 naïve subjects (mean age: 28.4 years, range: 23–41 years) participated in the experiments. They all had normal or corrected-to-normal visual acuity. Prior to the experiments all participants gave their informed consent according to the guidelines of the University of Trento ethical committee.

APPARATUS

Stimuli were generated on a PC running Matlab and Psychtoolbox 3.0 (Brainard, 1997; Pelli, 1997). They were presented on a 21″ Phillips Brilliance 109P4 CRT monitor with a refresh rate of 85 Hz and a screen resolution of 1280 × 1024 pixels. Except for the luminance of the monitor, the room was otherwise dark. Stimuli were viewed through a mirror stereoscope and a headrest was used to maintain a constant viewing distance of 60 cm.

STIMULI

Two square frames (8° visual angle) were presented on the display to help stabilize binocular fusion. Before subjects started the experiments the mirror stereoscope was manually adjusted until subjects achieved binocular fusion of the two frames and reported seeing only one single frame in their visual field. Throughout the experiments we used a circular black and white checkerboard as a target and a series of Mondrian masks to create CFS. The checkerboard target was 3 × 3° of visual angle in size and was formed by 12 equally sized sectors, each of which was further subdivided into four sections along the radius. The checkerboard was always presented at an eccentricity of 2° from the fixation point against a gray background (CIE coordinates: $x = 0.29$, $y = 0.32$, $z = 0.39$; luminance $= 18.2\ \mathrm{cd/m^2}$). Mondrians were created by randomly superimposing black, white and gray squares. Mondrians subtended 8° of visual angle and filled the entire inner area of the external frames (**Figure 1**). Prior to each experimental session 40 Mondrians were created and 10 of these were randomly selected for each trial. Checkerboards were presented to the right eye while Mondrians were always presented to the left eye.

PROCEDURES

In all experiments the subjects' task was to detect and report the location of the checkerboard target. Targets were presented for 24 ms (two video frames) in Experiments 1–3, and with variable durations during Experiment 4. Checkerboards changed luminance polarity (white areas turning black and black areas turning white) on their second frame of presentation (**Figure 1**). Each trial lasted 1.5 s, during which Mondrians were presented at their corresponding frequency (see below).

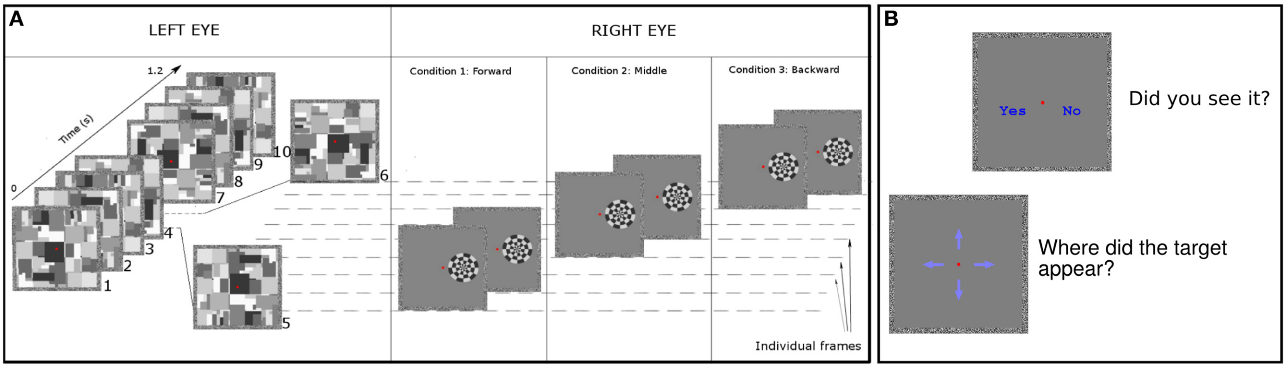


FIGURE 1 | Experimental design. (A) We presented Mondrian patterns to left eye of subjects (leftmost panel in the figure) at frequency of 8.5 Hz in Experiment 1. For Experiment 2 we used a range of frequencies. Targets were always displayed to the right eye of subjects. As an example, we show three trials occurring between the 5th and 6th Mondrian presentation. *Forward condition*: we displayed targets on the screen in the following two frames (∼24 ms) after the Mondrian. *Middle condition*: we presented targets at an equal temporal distance between the previous and subsequent Mondrian. *Backward condition*: we displayed targets for two frames before displaying the Mondrian. In all conditions the Mondrian's luminance polarity changed from the first frame to the second frame (see Materials and Methods Section). **(B)** On each trial, after the stimulus presentation we asked subjects to (1) report the location of the target on the screen and (2) to indicate whether they had perceived the target among the Mondrian sequence.

Objective detection

At the end of each trial four blue arrows appeared on the screen and participants had to indicate the location where the checkerboard had been presented on the screen. They responded "up," "down," "left" or "right" in a 4 alternative forced choice (AFC) using the four arrow keys of the keyboard (**Figure 1B**).

Subjective visibility

Immediately after the 4AFC subjects were presented with two options: "yes" or "no" to inquire whether or not they had perceived the target. This 2AFC provided a trial-by-trial subjective measure of target visibility. To avoid expectation biases we randomly varied the inter-trial intervals among the values of 250, 500, 750, or 1000 ms. Prior to the main experiment subjects performed two training block (one in Experiment 4). Results from the training blocks were excluded from data analysis.

EXPERIMENT 1. THE TIME COURSE OF MASKING WITH CFS

Twelve subjects (three authors) participated in Experiment 1. Mondrians were presented at a frequency of 8.5 Hz. Checkerboards were presented within a time window of 500–900 ms after trial onset. At least 5 Mondrians were presented on the screen before the appearance of the checkerboard. Targets appeared after the 5th, 6th, 7th, or 8th Mondrian. Checkerboards were presented at 4, 12, 16, 24, and 64% of Michelson contrast. To study the effect that temporal distance between checkerboard and Mondrian presentation had on target detection we presented three different timing conditions (**Figure 1**). In the 'backward' condition checkerboards were presented on the two video frames immediately preceding the presentation of a new Mondrian. In the "middle" condition, the target was presented on the two video frames temporally situated in the middle between two Mondrians. In the "forward" condition, targets were presented on the two video frames immediately following the presentation of a Mondrian.

In addition to the three timing conditions, we included a condition in which targets were always presented between the 2nd and 3rd Mondrian, mimicking the "middle" condition but at the beginning of the train of Mondrians. This condition allowed us to investigate the role of the initial train of Mondrians, since in previous studies it was hypothesized that suppression might build up in strength with repeated flashing of the Mondrians (CFS) compared to only one or a few flashes (Tsuchiya et al., 2006). Each subject performed 64 trials for each contrast and timing condition in 6 counterbalanced blocks of 160 trials amounting to a total of 960 trials (∼1 h of experiment). Sixteen checkerboards were presented in each location for each contrast × timing condition.

EXPERIMENT 2. THE EFFECTS OF MASK FREQUENCY ON TARGET SUPPRESSION

Twelve subjects (three authors) participated in Experiment 2. The main goal of this experiment was to assess the effect of mask frequency on the detection of brief targets. For this reason we presented the Mondrians at five temporal frequencies: 5.3, 8.5, 10.6, 16.6, and 28.5 Hz. The checkerboards were presented at 12 and 16% of Michelson contrast. We presented the checkerboards only in the backward condition (**Figure 1**). Targets appeared after the 5th, 6th, 7th, or 8th Mondrian. Each subject performed 40 trials for each contrast x Mondrian frequency, in 5 counterbalanced blocks of 80 trials amounting to a total of 400 trials (∼35 min of experiment). Each frequency was tested in a block and the order of presentation of blocks was randomized across subjects to avoid learning effects. A total of 10 checkerboards were presented in each location for each contrast × timing condition.

EXPERIMENT 3. COMPARING CFS AND INTER-OCULAR "SANDWICH" MASKING

Twelve subjects (one author) participated in this experiment. We aimed to evaluate the depth of suppression induced by CFS as compared to a brief inter-ocularly presented "sandwich" (forward plus backward) mask for the detection of briefly presented targets. All contrast and Mondrian frequency parameters were identical to Experiment 2, except that only two Mondrians (one preceding and one following the target) were presented on each trial. Apart from the differences in the number of Mondrian masks presented, the other parameters, i.e., the number of trials, blocks, conditions, and total duration of the experiment were identical to Experiment 2.

EXPERIMENT 4. BRIEF vs. PROLONGED TARGET PRESENTATION

Twelve subjects participated in this experiment. One of the subjects had to be discarded from further analysis as he claimed to be unable to detect/see any targets during the experiment. The main goal of this experiment was to assess the effect of target duration on the detection of targets. Targets were presented for 24, 48, 70, 118, and 506 ms. They changed polarity only once after the first video frame. We presented Mondrians at three temporal frequencies: 8.5, 16.6, and 28.5 Hz. The checkerboards were presented at 12% of Michelson contrast and they appeared after the 5th, 6th, 7th, or 8th Mondrian. Each subject performed 40 trials for each target duration × Mondrian frequency, in 10 counterbalanced blocks of 60 trials amounting to a total of 600 trials (∼45 min of experiment). All conditions were presented intermixed in each block. A total of 10 checkerboards were presented in each location for each target duration × Mondrian frequency condition.

ANALYSES

In all four experiments we assessed subjects' objective performance, subjective visibility reports and metacognition. We calculated *objective performance* as the proportion of correct responses in the 4AFC and we assessed *subjective visibility* as the proportion of "seen" trials in the 2AFC. By metacognition we mean the ability of subjects to discriminate between their own correct and incorrect responses when they claim to see the targets. In order to obtain a measure of metacognition we used the subjects' binary confidence ratings of their own responses (i.e., the "yes, target seen"/"no, target not seen" responses). First, we divided subjects' responses into two groups: correct and incorrect responses. Second, we calculated the proportion of correct trials "seen" and of incorrect trials "seen." We considered "seen" responses as analogous to "high confidence" responses in previous studies (Kunimoto et al., 2001). Third, we calculated hit rates as the proportion of seen and correct trials over all correct responses, and false alarm rates as the proportion of seen and incorrect responses over all incorrect responses. From these hit and false alarm rates we calculated d primes for each subject. This measure of metacognition is known as the type II d prime (Kunimoto et al., 2001).

RESULTS

EXPERIMENT 1

We studied the effects of the three timing conditions within CFS (backward, forward, and middle, see Materials and Methods) on objective accuracy, subjective reports and metacognition (**Figure 2A**). First, we assessed subjects' objective performance for target detection employing Two-Way repeated measures ANOVA, with timing condition and contrast as factors. We observed main effects for contrast, $F_{(4,\ 44)} = 56.01$, $p < 0.001$, partial eta-squared (N_P^2) $= 0.83$, and timing condition, $F_{(2,\ 22)} = 17.60$, $p < 0.001$, $N_P^2 = 0.61$, as well as a significant interaction parameter, $F_{(8,\ 88)} = 4.17$, $p = 0.002$. *Post-hoc* Bonferroni corrected paired t-tests showed a statistical difference between backward and middle masking conditions at 12 and 16% contrast levels ($t = -3.22$, $df = 11$, $p = 0.008$; and $t = -3.61$, $df = 11$, $p = 0.004$, respectively). Second, we measured subjective visibility by counting the proportion of targets reported as seen in the 2AFC. We observed a main effect for contrast, $F_{(4,\ 44)} = 52.70$, $p < 0.001$, for timing condition, $F_{(2,\ 22)} = 11.6$, $p < 0.001$, $N_P^2 = 0.82$, and a significant interaction parameter $F_{(8,\ 88)} = 5.7$, $p < 0.001$, $N_P^2 = 0.34$. We did not observe any statistical difference among timing conditions (**Figure 2B**, *post-hoc* Bonferroni corrected paired t-tests). Finally, we assessed subjects' metacognition (**Figure 2C**). We observed a main effect for contrast, $F_{(4,\ 44)} = 23.80$, $p < 0.001$, $N_P^2 = 0.68$, on type II d primes, but no effect for the timing conditions, $F_{(2,\ 22)} = 1.50$, $p = 0.247$, nor for the interaction parameter, $F_{(8,\ 88)} = 0.26$, $p = 0.960$. To directly compare objective performance, subjective visibility and metacognition we computed the z-score of each dependent

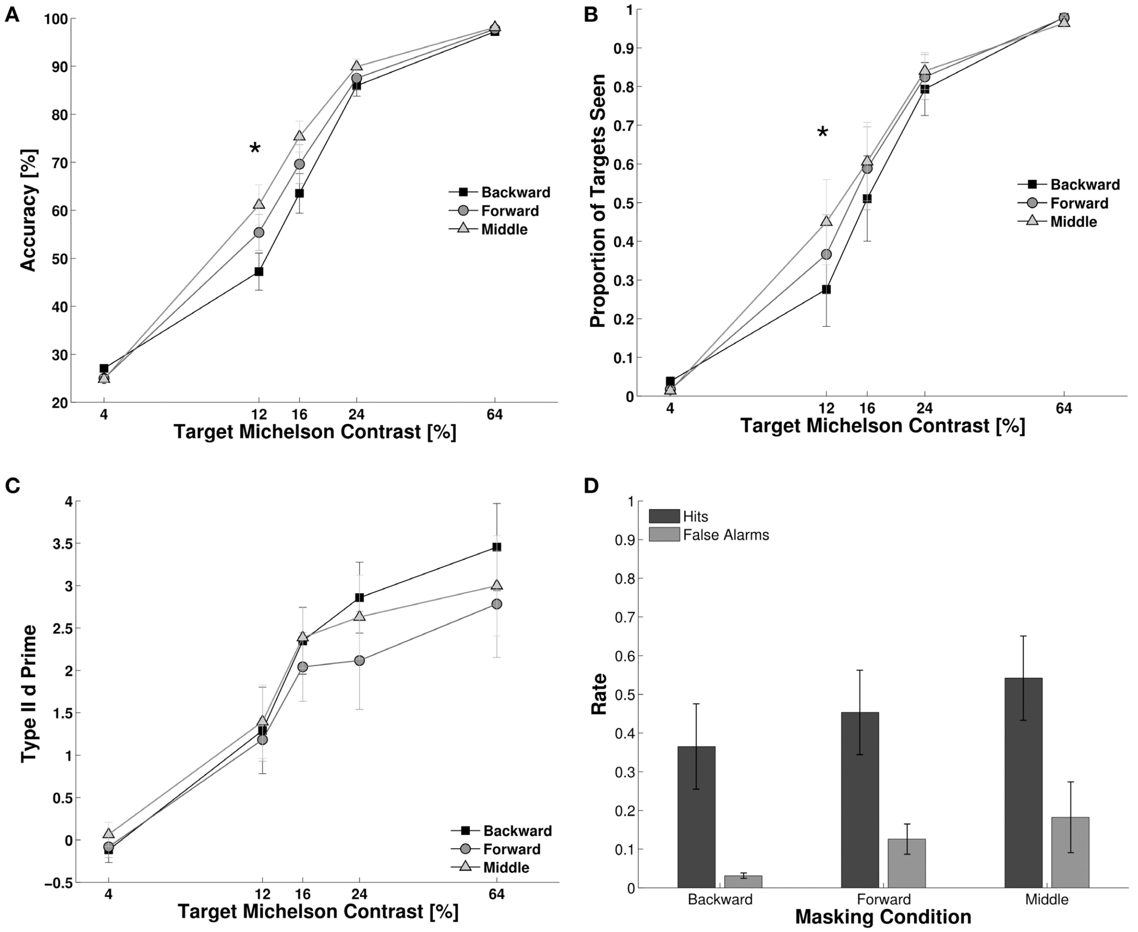


FIGURE 2 | Experiment 1. We studied the effect of our experimental conditions on target suppression. **(A–C)** Lower performance indicates higher suppression. **(A)** Objective performance for target detection. The effect of suppression was strongest for the backward masking condition. Subjects were more accurate in the middle condition than in the backward masking conditions for the 12 and 16% contrast levels. **(B)** Target visibility showed a similar trend as to objective performance, subjects reported to see more targets in the middle condition than in the backward condition. **(C)** Metacognition was equivalent for the three masking conditions at all contrast levels (see statistics in the Results Section). **(D)** Hit and false alarm rates for trials where subjects reported to consciously see the target. The panel shows the 3 masking conditions at 12% contrast level. The linear increase in the proportion of targets that subjects reported as "seen" across masking conditions was correlated with an increase in hits rate, but also with an increase in the false alarm rates. This resulted in an equivalent metacognition across masking conditions. $N = 12$, error bars represent one s.e.m. Asterisks indicate $p < 0.05$ (corrected for multiple comparisons, see Results Section).

variable across all conditions and participants. Using this normalized measure we computed the difference between "middle masking condition" and "backward masking condition" for each participant and dependent variable. Significance was assessed by a within participant ANOVA, with variable type as the independent variable, $F_{(2,\ 22)} = 9.103$, $p = 0.001$, $N_P^2 = 0.44$. Bonferroni corrected *post-hoc* analysis revealed a difference between subjective visibility and metacognition, $t_{(11)} = 3.09$, $p = 0.02$, and between objective performance and metacognition, $t_{(11)} = 3.41$, $p = 0.01$ (see **Supplementary Figure 1**).

The pattern of data showed that masking types affected objective performance and visibility reports at 12 and 16% of contrast levels. However, metacognition did not vary with masking condition (**Figure 2D**). This suggests that the ability of subjects to discriminate between their own correct and incorrect responses remained equal across masking conditions in spite of the increases in objective performance for the middle condition. Even though subjects were more accurate and reported seeing more targets in the middle than in the backward conditions at 12 and 16% of contrast levels, the hit and false alarm rates increased proportionally when subjects claimed to see the target. For the 12% contrast level we observed a main effect of masking condition, $F_{(2,\ 22)} = 12.10$, $p < 0.001$, $N_P^2 = 0.52$, a main effect of response type [hit rate vs. false alarm rate, $F_{(1,\ 11)} = 16.9$, $p < 0.001$, $N_P^2 = 0.60$] but no significant interaction parameter, $F_{(2,\ 22)} = 0.06$, $p = 0.87$. The linear increase in hits and false alarms results in identical type II d primes across conditions, which indicates that subjects had a better objective performance at detecting targets without an increase in their metacognition, i.e., without being more accurate in their judgments about their own correct and incorrect responses.

EXPERIMENT 2

As expected, the frequency of presentation of Mondrians affected all three measures, but we found that performance generally decreased as a function of frequency. For objective performance at detecting the target (**Figure 3A**) we observed a main effect of frequency, $F_{(4,\ 44)} = 12.50$, $p < 0.001$, $N_P^2 = 0.53$, and a main effect of contrast, $F_{(1,\ 11)} = 76.80$, $p < 0.001$, $N_P^2 = 0.87$, with no interaction between these main factors, [$F_{(4,\ 44)} = 1.46$, $p < 0.232$]. Subjective reports of visibility (**Figure 3B**) also decreased

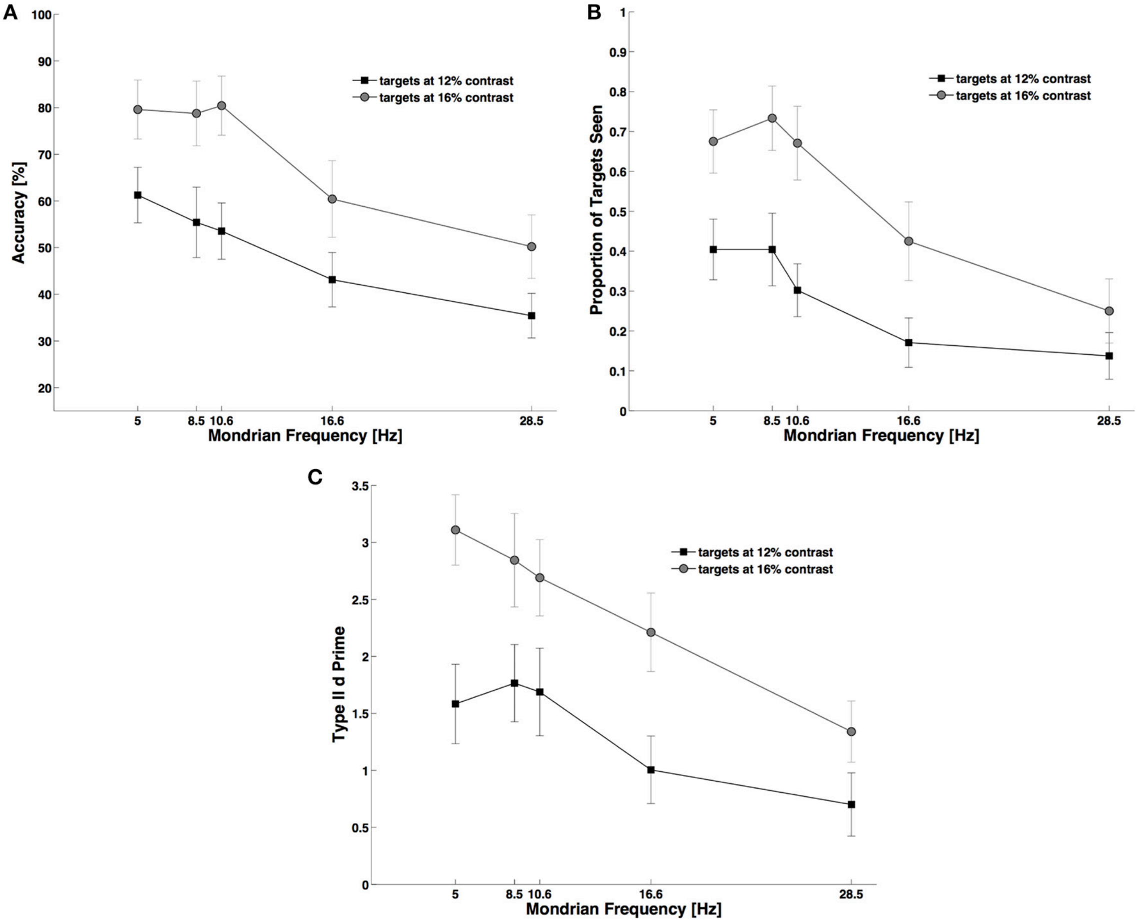


FIGURE 3 | Experiment 2. During CFS higher Mondrian frequencies generated stronger suppression of targets and a decrease in subjects' performance. The same decaying trend equally affected: objective performance **(A)**, subjective reports of visibility **(B)**, and metacognition **(C)**. For this experiment we used only trials in the backward condition (see **Figure 1** and Materials and Methods Section). As with **Figure 1**, in (**A–C**) lower performance indicates higher suppression from the Mondrian masks.

with decreasing contrast, $F_{(1,\ 11)} = 46.60, p < 0.001, N_P^2 = 0.80$, and with increasing Mondrian frequencies, $F_{(4,\ 44)} = 16.40$, $p < 0.001$, $N_P^2 = 0.59$, and we found a significant interaction parameter for these factors, $F_{(4,\ 44)} = 5.68, p = 0.001, N_P^2 = 0.34$. *Post-hoc* Bonferroni corrected comparisons showed that visibility for the two contrast values differed across all Mondrian frequencies except at the highest (28.5 Hz) frequency tested. The analysis of metacognition (**Figure 3C**) showed again an expected main effect of contrast, $F_{(1,\ 11)} = 39.70, p < 0.001, N_P{}^2 = 0.78$, and of Mondrian frequency, $F_{(4,\ 44)} = 9.25$, $p < 0.001$, $N_P^2 = 0.45$, on type II d prime, but no interaction parameter, $F_{(4,\ 44)} = 1.47, p = 0.230$. In conclusion, higher frequencies caused a consistent decrease in subjects' objective performance, subjective visibility ratings and metacognition.

EXPERIMENT 3

From Experiment 2, it remains unclear whether the effect of the Mondrian frequencies on subjects' performance is due to the overall frequency of presentation of Mondrians or to the decreasing gap between the Mondrian that would place the targets temporally closer to their preceding and following Mondrians. We ran the following experiment in order to determine which of these two possibilities was causing the decreases in performance and the increases in suppression.

As shown in **Figure 4**, during dichoptic masking subjects' objective performance varied with Mondrian frequency, $F_{(4,\ 44)} = 5.93$, $p = 0.03$, $N_P{}^2 = 0.35$, and contrast, $F_{(1,\ 11)} = 12.00$, $p = 0.005$, $N_P{}^2 = 0.52$, (**Figure 4A**). We also observed an interaction between these main factors, $F_{(4,\ 44)} = 2.71$, $p = 0.045$, $N_P{}^2 = 0.19$. When we analyzed the effect of dichoptic masking on target visibility we found that both contrast, $F_{(1,\ 11)} = 13.30$, $p = 0.003$, $N_P{}^2 = 0.54$, and Mondrian frequency, $F_{(4,\ 44)} = 5.37, p = 0.002$, had an effect on target visibility, and that there was an interaction between the two factors, $F_{(4,\ 44)} = 4.94$, $p = 0.004$, $N_P{}^2 = 0.31$. On the other hand, the analysis of metacognition showed a marginal but non-significant effect of Mondrian frequency on type II d primes, $F_{(4,\ 44)} = 2.48$, $p = 0.07$, and no main effect for contrast, $F_{(1,\ 11)} = 2.79$, $p = 0.123$, nor for an interaction between the Mondrian frequency and contrast, $F_{(4,\ 44)} = 0.68, p = 0.591$.

Interestingly, inter-ocular "sandwich" masking was actually more effective than the CFS method used in Experiment 2 (**Figure 3**). Subjects' overall objective performance decreased during dichoptic masking in Experiment 3 compared with CFS in

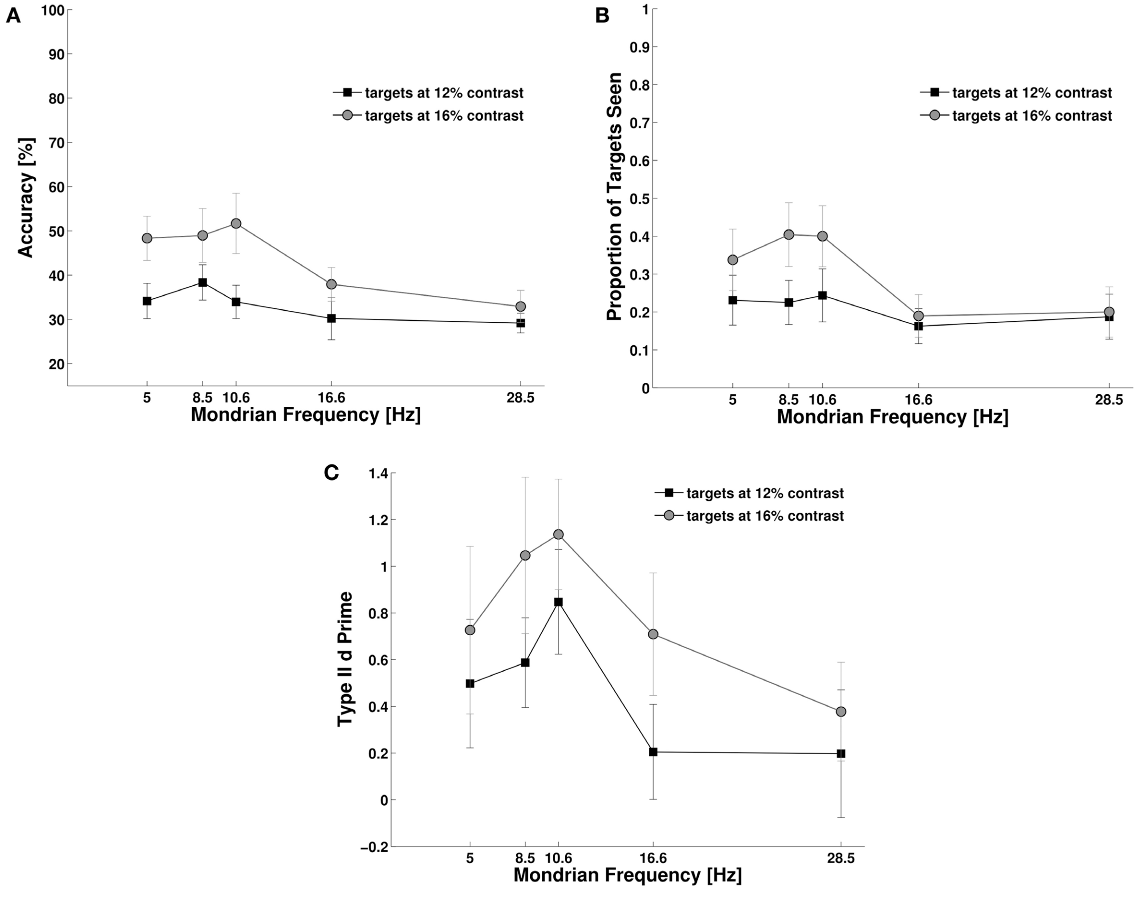


FIGURE 4 | Experiment 3. Control experiment using only two Mondrian masks ("Sandwich Masking"). This experiment generated stronger target suppression than Experiment 2 (**Figure 3**, see Results Section for statistics), suggesting that the temporal proximity of the Mondrian with the target constitutes the main cause of suppression of transient targets. **(A)** Objective performance, **(B)** Subjective reports of visibility, and **(C)** Metacognition.

Experiment 2. Average performance was computed for each participant in Experiment 2 (12 participants) and Experiment 3 (12 participants) and the two groups were compared using a two-sample *t*-test: $t_{(22)} = 3.31, p = 0.003$, see **Figures 3**, **4**.

EXPERIMENT 4

We studied the effect of target duration and Mondrian frequency on objective accuracy, subjective reports and metacognition. First, we investigated subjects' objective performance for target detection. Objective performance moved from chance level to ceiling performance as target duration reached 70 ms (**Figure 5A**). A Two-Way repeated measures ANOVA, with target duration and Mondrian frequency as factors showed a main effect for target duration, $F_{(4,\ 40)} = 1.6$, $p < 0.001$, $N_P{}^2 = 0.91$, but only a marginal and statistically non-significant effect of Mondrian frequency, $F_{(2,\ 20)} = 2.90$, $p = 0.078$, $N_P{}^2 = 0.22$. However, we did observe a significant interaction parameter, $F_{(8,\ 80)} = 3.84$, $p < 0.01$, $N_P{}^2 = 0.27$. With the exception of the 48 ms condition, we could not observe any differences in the objective performance for each Mondrian frequency condition. For the 48 ms target duration condition we observed, in line with the results of Experiment 2, a better performance for lower frequencies than for higher masking frequencies (**Figure 5A**). This trend was larger between the 8.5 and the 28.5 Hz conditions ($t = 2.53$, $df = 10$, $p = 0.029$). Subjective reports of visibility (**Figure 5B**) also increased with target duration, $F_{(4,\ 40)} = 93.20$, $p < 0.001$, $N_P{}^2 = 0.90$, much in accordance with objective performance. Again, we did not observe a main effect of Mondrian Frequency, $F_{(2,\ 20)} = 2.73$, $p = 0.089$, $N_P{}^2 = 0.21$, but we found an interaction parameter between the factors, $F_{(8,\ 80)} = 5.38$, $p < 0.001$, $N_P{}^2 = 0.35$. As with objective performance, subjective reports were very low for the shortest target durations but they were at the ceiling of performance from 70 ms onwards. For the 48 ms condition, subjective reports were higher for the 8.5 Hz condition than for the 16 and 28 Hz condition. We observed a similar trend as with objective performance, in particular between the 8.5 and 28 Hz condition ($t = 2.80$, $df = 10$, $p = 0.018$). The analysis of metacognition (**Figure 5C**) showed again an expected main effect of target duration, $F_{(4,\ 40)} = 38.30$, $p < 0.001$, $N_P{}^2 = 0.79$, no effect of Mondrian frequency, $F_{(2,\ 20)} = 0.162$, $p = 0.85$, $N_P{}^2 = 0.01$ on type II d prime, but an interaction parameter, $F_{(8,\ 80)} = 4.20$, $p = 0.001$, $N_P{}^2 = 0.29$. Metacognition followed the same trend as objective performance and subjective reports, starting with a d prime of 0 for the 24 ms condition and reaching ceiling performance (d primes above 3) for the target durations of 70 ms or more. For the 48 ms condition, type II d primes were higher for the 8.5 and 16 Hz conditions than the 28 Hz condition ($t = 2.37$, $df = 10$, $p = 0.039$ and t = 2.40, $df = 10$, $p = 0.036$).

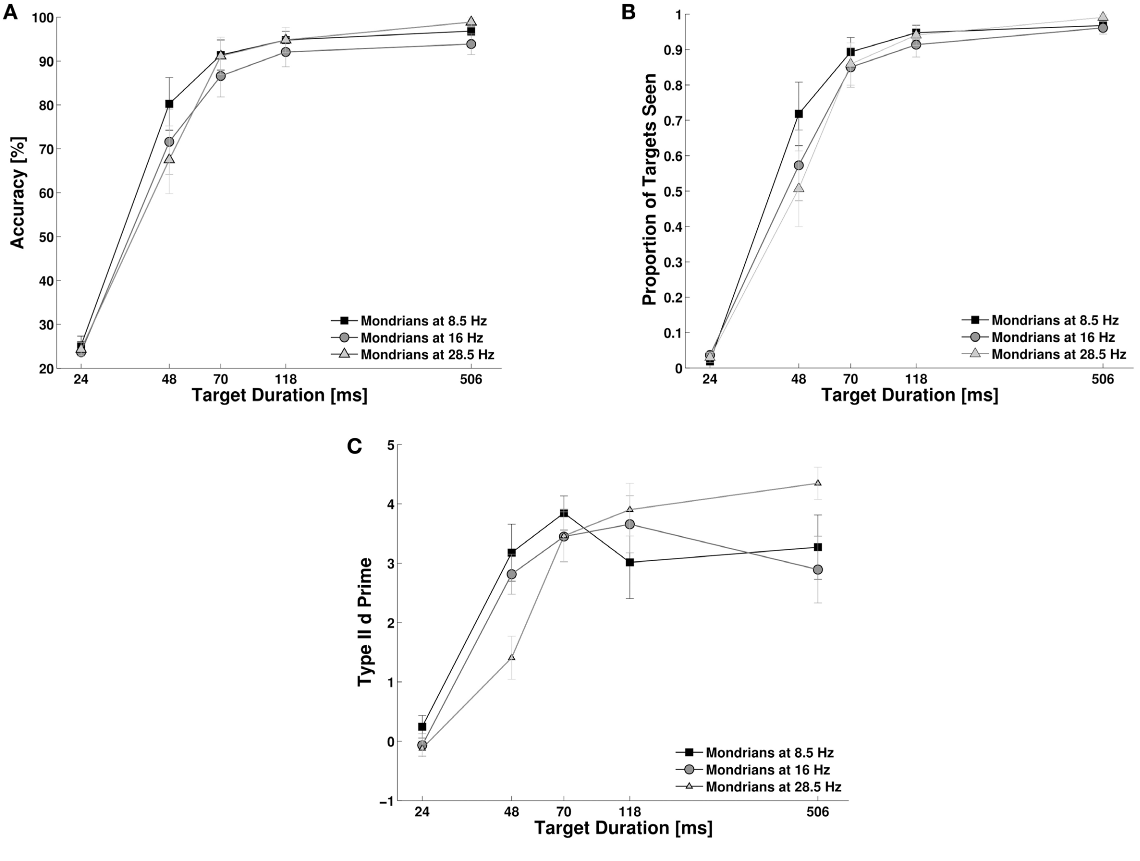


FIGURE 5 | Experiment 4. Target duration modulated inter-ocular suppression during CFS and affected objective performance **(A)**, subjective reports of visibility **(B)**, and metacognition **(C)**.

Overall, longer target durations caused a consistent increase in subjects' objective performance, subjective visibility ratings and metacognition. This increase showed a steep slope, subjects' performances went from chance level at 24 ms and reached near ceiling values at 70 ms target duration. Even though this modulation by target duration was irrespective of Mondrian frequency, at 48 ms target duration, we could observe that lower Mondrian frequencies generated better performance (confirming the results obtained in Experiment 2).

DISCUSSION

We showed that the temporal onset asynchrony between targets and Mondrians as well as the mask frequency both influence the strength of CFS for transient target stimuli. Smaller stimulus onset asynchronies (SOA) between Mondrians and targets generate stronger suppression (the forward and backward conditions in Experiment 1, see **Figure 1A**). Our results suggest that for transient targets CFS shows a trend of suppression similar to that reported in dichoptic visual masking (Macknik et al., 2000), flash suppression (Wolfe, 1984) and models of visual masking (Breitmeyer and Öğmen, 2006).

During CFS the depth of inter-ocular suppression varies depending on the spatial properties of the targets and Mondrians (Yang and Blake, 2012). We found that the temporal frequencies of Mondrians also influence the suppression of brief targets: higher temporal frequencies generated stronger suppression than lower frequencies. This modulation by Mondrian frequency occurred for CFS (Experiment 2) and for the brief presentation of only two Mondrians during "sandwich" masking (Experiment 3). Interestingly, "sandwich" masking resulted in the strongest suppression across all of the experiments, indicating that for brief target stimuli suppression was stronger for dichoptic masking than for CFS. These results, in addition to the fact that CFS constitutes the strongest technique for suppressing prolonged stimuli (Tsuchiya and Koch, 2005; Tsuchiya et al., 2006) suggest separate mechanisms of suppression operating for brief and prolonged stimuli (see below). An alternative interpretation of the finding that inter-ocular sandwich masking results in stronger suppression than CFS is that during CFS subjects might have established a temporal rhythm to facilitate the transient target detection. In our experiments we controlled for the effect of temporal attention on target detection by jittering target presentation time with regards to the onset time of Mondrians (which created a temporal uncertainty around target onset, see Materials and Methods Section). However, this jitter might not have been enough to fully discard the possibility of subjects establishing a temporal rhythm during the presentation of the Mondrians. Further studies are needed to clarify this point and to explain why, even if we consider plausible the hypothesis of an entrainment of attention, higher frequencies still generated stronger suppression of targets than lower frequencies.

Our results are consistent with a visual masking model that separates between a "sustained" and a "transient" channel for the detection of prolonged and transient stimuli (Breitmeyer and Öğmen, 2006). In this model brief targets are detected through the "transient channel" as triggered by the spatiotemporal edges of a stimulus (Macknik et al., 2000), while prolonged targets break into consciousness due to the "sustained channel" including more internally driven inhibition/adaptation and stochastic processes (Brascamp et al., 2006; Tsuchiya et al., 2006). The model starts from the anatomical distinction between Parvocellular (P) and Magnocellular (M) pathways in the retina toward lateral geniculate nucleus (LGN) and primary visual cortex. The two afferent streams are anatomically separated at the LGN level as well as at the input level of primary visual cortex (Lund, 1988; Callaway, 1998) and they show clear functional specialization (Croner and Kaplan, 1995). While the M pathway shows low contrast threshold, high luminance-contrast gain and short latency responses to visual stimuli (transient channel), the P pathway exhibits higher contrast thresholds, low contrast gain and sustained responses (Schmolesky et al., 1998). Crucially, the M pathway signals the appearance of stimuli and the rapid changes of location (motion) over time whereas the P pathway primarily signals pattern aspects such as the contours of stationary or slowly moving stimuli (Breitmeyer and Öğmen, 2006).

The model assumes that a mask that rapidly follows a visual stimulus interferes with the stimulus elaboration that would otherwise be performed by the transient channel, impeding visual stimuli detection. In this framework, CFS can be interpreted as a repeated resetting of the transient channel, resulting in decreased detection performance for brief visual stimuli presented together with the mask train (24–48 ms, see **Figure 5**). This is in line with the proposal that CFS does not constitute a stronger version of binocular rivalry, but a continuous repetition of flash suppression where each independent flash of Mondrian resets and renews inter-ocular suppression (Tsuchiya et al., 2006). It also suggests two types of masking mechanisms: a within-transient-channel masking for the suppression of transient targets with abrupt onsets and a between-transient-and-sustained channel masking for prolonged targets. Most previous studies using CFS have achieved long periods of invisibility of target stimuli (in the order of seconds) by adopting increasing ramps of contrast for the targets (Tsuchiya and Koch, 2005; Tsuchiya et al., 2006; Hesselmann and Malach, 2011; Stein and Sterzer, 2011; Stein et al., 2011). In our experiment 4, however, we show that targets with an abrupt onset break suppression with durations as short as 40 ms. We can explain the discrepancy between previous experiments with prolonged stimuli and our experiments with brief stimuli if we consider that the gradual ramp-up of the target contrast reduces the involvement of the transient channel. We hypothesize that since the transient channel plays an important role in the recruitment of the sustained channel, the latter does not get immediately activated. The train of masks leaves sustained targets presented with a ramp of contrast relatively unaltered, suggesting that in these cases the sustained channel (less affected by the Mondrians) performs target detection. Presumably, this yields long and stable suppression of the target stimuli. The sudden onset of counter-phase target stimuli in our experiments might have overcome the masking power of the CFS train at $\sim$40 ms (Experiment 4), as would be expected given the higher sensitivity for flicker detection that characterizes the transient channel (Tolhurst, 1973).

Our findings show that the spatiotemporal dynamics of CFS affect stimuli visibility and cause differences among objective performance, subjective reports and metacognition. Previous research has shown that objective performance with near-threshold stimuli can be above chance level with little or no awareness of the presence of the target (Cheesman and Merikle, 1986; Kunimoto et al., 2001). In our experiments, visibility ratings remained in close agreement with objective discrimination accuracy. As shown in Experiment 1, subjects became more accurate and reported seeing the target more often for the "middle" condition compared to the "backward" condition. However, subjects' metacognition did not increase with visibility reports. While subjects became more accurate (objective sensitivity improved) and reported more targets as "seen," they also made more errors with regard to their own judgments. This divergence between subjective and objective measures of visual awareness (see **Figure 1**) supports the idea that for stimuli presented near the threshold of visibility, metacognition often lags behind objective accuracy and subjective reports (Kunimoto et al., 2001).

In conclusion, our experiments extend the study of the interactions between inter-ocular masking and CFS. They provide a better understanding of the dynamics of CFS with transient onset stimuli and of the robust similarities between transient target CFS and dichoptic visual masking. Changes in CFS dynamics that render stimuli more or less visible may cause differences among objective performance, subjective reports and metacognition. As our study shows, generalization is often not easy to achieve since a number of related mechanisms of visual perception can summate in different ways for each specific masking technique. For this reason, we stress the need for a careful consideration of the type of psychophysical techniques employed, the way subjects' responses are interpreted, and the type of stimuli being rendered invisible before comparing results among studies and inferring non-conscious processes.

ACKNOWLEDGMENT

David Melcher was supported by the European Research Council (ERC grant agreement no. 313658).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fpsyg.2014.00804/abstract

Supplementary Figure 1 | We compared objective performance, visibility and metacognition within Experiment 1. The different measures were normalized by computing the z-score of each dependent variable across all conditions and participants. Using this normalized measure we computed the difference between "middle mask condition" and "backward condition" for each participant and dependent variable. The average difference is reported across the 3 dependent variables (see x axis labels). The difference between "middle mask condition" and "backward condition" obtained with normalized objective performance is significantly different than with normalized metacognition ($p < 0.05$). Moreover, the difference between "middle mask condition" and "backward condition" obtained with normalized visibility is significantly different than with normalized metacognition ($p < 0.05$, see main text for details).

REFERENCES

Alais, D., and Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. *Vision Res.* 47, 269–279. doi: 10.1016/j.visres.2006.09.003

Blake, R., and Fox, R. (1974). Binocular rivalry suppression: insensitive to spatial frequency and orientation change. *Vision Res.* 14, 687–692. doi: 10.1016/0042-6989(74)90065-0

Brainard, D. H. (1997). The psychophysics toolbox. *Spat. Vis.* 10, 433–436. doi: 10.1163/156856897X00357

Brascamp, J. W., van Ee, R., Noest, A. J., Jacobs, R. H., and van den Berg, A. V. (2006). The time course of binocular rivalry reveals a fundamental role of noise. *J. Vis.* 6, 1244–1256. doi: 10.1167/6.11.8

Breitmeyer, B. G., and Öğmen, H. (2006). *Visual Masking: Time Slices Through Conscious and Unconscious Vision*. Oxford: Oxford University Press. doi: 10.1093/acprof:oso/9780198530671.001.0001

Callaway, E. (1998). Local circuits in primary visual cortex of the macaque monkey. *Annu. Rev. Neurosci.* 21, 47–74. doi: 10.1146/annurev.neuro.21.1.47

Cheesman, J., and Merikle, P. M. (1986). Distinguishing conscious from unconscious perceptual processes. *Can. J. Psychol.* 40, 343. doi: 10.1037/h0080103

Croner, L. J., and Kaplan, E. (1995). Receptive fields of P and M ganglion cells across the primate retina. *Vision Res.* 35, 7–2. doi: 10.1016/0042-6989(94)E0066-T

Faivre, N., Berthet, V., and Kouider, S. (2014). Sustained invisibility through crowding and continuous flash suppression: a comparative review. *Front. Psychol.* 5:475. doi: 10.3389/fpsyg.2014.00475

Fogelson, S. V., Kohler, P. J., Miller, K. J., Granger, R., and Tse, P. U. (2014). Unconscious neural processing differs with method used to render stimuli invisible. *Front. Psychol.* 5:601. doi: 10.3389/fpsyg.2014.00601

Hesselmann, G., and Malach, R. (2011). The Link between fMRI-BOLD activation and perceptual awareness is "Stream-Invariant" in the human visual system. *Cereb. Cortex* 21, 2829–2837. doi: 10.1093/cercor/bhr085

Izatt, G., Dubois, J., Faivre, N., and Koch, C. (2014). A direct comparison of unconscious face processing under masking and interocular suppression. *Front. Psychol.* 5:659. doi: 10.3389/fpsyg.2014.00659

Kaunitz, L., Fracasso, A., Lingnau, A., and Melcher, D. (2013). Non-conscious processing of motion coherence can boost conscious access. *PLoS ONE* 8:e60787. doi: 10.1371/journal.pone.0060787

Kaunitz, L., Fracasso, A., and Melcher, D. (2011). Unseen complex motion is modulated by attention and generates a visible aftereffect. *J. Vis.* 11:10. doi: 10.1167/11.13.10

Kim, C.-Y., and Blake, R. (2005). Psychophysical magic: rendering the visible 'invisible.' *Trends Cogn. Sci.* 9, 381–388. doi: 10.1016/j.tics.2005.06.012

Kunimoto, C., Miller, J., and Pashler, H. (2001). Confidence and accuracy of near-threshold discrimination responses. *Conscious. Cogn.* 10, 294–340. doi: 10.1006/ccog.2000.0494

Lin, Z., and He, S. (2009). Seeing the invisible: the scope and limits of unconscious processing in binocular rivalry. *Prog. Neurobiol.* 87, 195–211. doi: 10.1016/j.pneurobio.2008.09.002

Lund, J. (1988). Anatomical organization of macaque monkey striate visual cortex. *Annu. Rev. Neurosci.*11, 253–288. doi: 10.1146/annurev.ne.11.030188.001345

Macknik, S. L., Martinez-Conde, S., and Haglund, M. M. (2000). The role of spatiotemporal edges in visibility and visual masking. *Proc. Natl. Acad. Sci. U.S.A.* 97, 7556–7560. doi: 10.1073/pnas.110142097

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat. Vis.* 10, 437–442. doi: 10.1163/156856897X00366

Schiller, P. H., and Smith, M. C. (1968). Monoptic and dichoptic metacontrasf. *Percept. Psychophys.* 3, 237–239. doi: 10.3758/BF03212735

Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Leventhal, J. D., et al. (1998). Signal timing across the macaque visual system. *J. Neurophysiol.* 79, 3272–3278.

Stein, T., Hebart, M., and Sterzer, P. (2011). Breaking continuous flash suppression: a new measure of unconscious processing during interocular suppression? *Front. Hum. Neurosci.* 5:167. doi: 10.3389/fnhum.2011.00167

Stein, T., and Sterzer, P. (2011). High-level face shape adaptation depends on visual awareness: evidence from continuous flash suppression. *J. Vis.* 11:5. doi: 10.1167/11.8.5

Tolhurst, D. J. (1973). Separate channels for the analysis of the shape and the movement of moving visual stimulus. *J. Physiol.* 231, 385–402.

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Tsuchiya, N., Koch, C., Gilroy, L., and Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *J. Vis.* 6, 1068–1078. doi: 10.1167/6.10.6

van Boxtel, J., Tsuchiya, N., and Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. *Proc. Natl. Acad. Sci. U.S.A.* 107, 8883–8888. doi: 10.1073/pnas.0913292107

Wheatstone, C. (1838). Contributions to the physiology of vision. part the first. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philos. Trans. R. Soc. Lond.* 128, 371–394. doi: 10.1098/rstl.1838.0019

Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Res.* 24, 471–478. doi: 10.1016/0042-6989(84)90044-0

Yang, E., and Blake, R. (2012). Deconstructing continuous flash suppression. *J. Vis.* 12:8. doi: 10.1167/12.3.8

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 13 February 2014; accepted: 07 July 2014; published online: 30 July 2014.
Citation: Kaunitz LN, Fracasso A, Skujevskis M and Melcher D (2014) Waves of visibility: probing the depth of inter-ocular suppression with transient and sustained targets. Front. Psychol. ***5****:804. doi: 10.3389/fpsyg.2014.00804*
This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 11 September 2014
doi: 10.3389/fpsyg.2014.00969

Comparing unconscious processing during continuous flash suppression and meta-contrast masking just under the limen of consciousness

Ziv Peremen[1,2] **and Dominique Lamy**[1,2] *

[1] The School of Psychology Sciences, Tel Aviv University, Tel Aviv, Israel
[2] The Sagol School of Neuroscience, Tel Aviv University, Tel Aviv, Israel

Edited by:
Nathan Faivre, California Institute of Technology, USA

Reviewed by:
Thomas Schmidt, University of Kaiserslautern, Germany
Eva Van Den Bussche, Vrije Universiteit Brussel, Belgium

***Correspondence:**
Dominique Lamy, The School of Psychology Sciences and The Sagol School of Neuroscience, Tel Aviv University, Ramat Aviv, P. O. Box 39040, Tel Aviv 69978, Israel
e-mail: domi@post.tau.ac.il

Stimuli can be rendered invisible using a variety of methods and the method selected to demonstrate unconscious processing in a given study often appears to be arbitrary. Here, we compared unconscious processing under continuous flash suppression (CFS) and meta-contrast masking, using similar stimuli, tasks and measures. Participants were presented with a prime arrow followed by a target arrow. They made a speeded response to the target arrow direction and then reported on the prime's visibility. Perception of the prime was made liminal using either meta-contrast masking (Experiment 1) or CFS (Experiments 2 and 3). Conscious perception of the prime was assessed using a sensitive visibility scale ranging from 0 to 3 and unconscious processing was measured as the priming effect on target discrimination performance of prime-target direction congruency when prime visibility was null. Crucially, in order to ensure that the critical stimuli were equally distant from the limen of consciousness, we sought stimulus and temporal parameters for which the proportion of 0-visibility trials was comparable for the two methods. We found that the method used to prevent conscious perception matters: unconscious processing was substantial with meta-contrast masking but absent with CFS. These findings suggest that CFS allows very little perceptual processing, if at all, and that previous reports of high-level and complex unconscious processing during CFS may result from partial awareness.

Keywords: conscious perception, unconscious perception, subliminal processing, meta-contrast masking, continuous flash suppression, response priming, awareness, consciousness

INTRODUCTION

Visual consciousness has been the focus of intense research in the last two decades (Marcel, 1983; Erdelyi, 1986, 2004; Greenwald et al., 1996; Vorberg et al., 2003; Ramsøy and Overgaard, 2004; Lau and Passingham, 2006; Schmidt and Vorberg, 2006; Lamy et al., 2009; Sandberg et al., 2010). The search for the limits of unconscious processing lies at the heart of this research: which processes can unfold in the absence of conscious perception and conversely, for which processes is consciousness essential? In other words, what is the function of consciousness? The most widely used empirical strategy used to address this question is to probe the influence on behavior of stimuli that are barred from conscious access, so as to assess what processes can be performed outside perceptual awareness.

A rather large arsenal of paradigms stand at disposal to prevent a visual stimulus from entering consciousness: pattern masking (e.g., Breitmeyer and Ganz, 1976), meta-contrast masking (Breitmeyer, 1978), object-substitution masking (Di Lollo et al., 2000), continuous flash suppression (CFS; Tsuchiya and Koch, 2005), the attentional blink (Raymond et al., 1992), inattentional blindness (Mack and Rock, 1998), and more (see Kim and Blake, 2005 for a review). The choice of the paradigm used to demonstrate unconscious processing often appears to be arbitrary, despite the fact that the different paradigms are known to affect perceptual processing in qualitatively different ways (e.g., Enns, 2004; Almeida et al., 2010; Kanai et al., 2010; Faivre et al., 2012; Fogelson et al., 2014). On the one hand, one could claim that the method used to prevent conscious perception should not matter as long as unconscious perception is demonstrated. On the other hand, however, it is important to minimize failures to identify processes that can be performed without consciousness. To do that, targeting the procedures that obliterate conscious processing while most minimally impairing unconscious processing would seem to be the most judicious strategy. To illustrate this point bluntly, blindfolding observers to prevent conscious perception would be a bad choice because it would also thoroughly eliminate unconscious processing.

In the present paper, we focused on a paradigm that has become increasingly popular in consciousness research: CFS (henceforth, CFS, Tsuchiya and Koch, 2005), and investigated the extent to which it disrupts unconscious processing. With this method, arrays of randomly generated shapes of different colors (Mondrians) presented successively at ~10 Hz to one eye can reliably suppress the conscious awareness of an image presented to the other eye. One of the main reasons for the enthusiasm surrounding CFS is that, unlike backward masking, which is effective only when the target is presented very briefly (typically for less that 100 ms), CFS-induced suppression can last very long, on the order of seconds (Shimaoka and Kaneko, 2011; Stein et al., 2011). Based on the premise that high-level computations may require relatively long processing times, CFS should be a particularly well-suited paradigm in order to measure high-level unconscious processing.

Consistent with this conjecture, several studies relying on breaking suppression during CFS have revealed that we are capable of performing complex, high-level cognitive operations without conscious perception (e.g., Jiang et al., 2006; Costello et al., 2009; Mudrik et al., 2011; Sklar et al., 2012; Lupyan and Ward, 2013). In a nutshell, the rationale underlying the use of breaking suppression is that if a stimulus is found to overcome (or break) suppression earlier than another stimulus, then one can conclude that the property on which the two stimuli differ was processed unconsciously. However, there has been no convincing evidence that differences in breaking suppression times reflect genuine unconscious processing rather than processing under partial consciousness (e.g., Stein et al., 2011; see Gayet et al., 2014).

Other CFS studies that either used a traditional dissociation procedure or examined the neural consequences of this method have generated conflicting findings as to whether CFS interferes with low-level or with high-level cognitive processing (see Sterzer et al., 2014 for a review). For instance, some authors showed that subliminal stimuli suppressed using CFS elicit semantic processing (e.g., Almeida et al., 2008, 2010; Bahrami et al., 2010), while others showed that CFS-suppressed stimuli undergo only low-level perceptual processing (e.g., Faivre et al., 2012). Likewise, while several functional MRI studies showed robust suppression of activity in higher visual areas during CFS (e.g., Fang and He, 2005; Jiang et al., 2006; Hesselmann and Malach, 2011) but not in the primary visual cortex (Watanabe et al., 2011), Yuval-Greenberg and Heeger (2013) recently showed that CFS does in fact modulate fMRI responses in the primary visual cortex (see also Kang et al., 2011 for consistent findings using ERP methodology).

Most crucially, however, the very few studies that directly compared the extent of unconscious processing when stimuli are rendered invisible using CFS vs. other methods, suggest that CFS has the lower hand: it actually elicits more restricted unconscious processing (Almeida et al., 2010; Faivre et al., 2012, 2014; Izatt et al., 2014). For instance, Faivre et al. (2012) showed that while emotional face primes biased subsequent preference judgments when suppressed from awareness by gaze-contingent crowding, they did not elicit such emotion-related processing when suppressed by backward masking or CFS. Instead, they only produced an effect akin to low-level perceptual adaptation: responses to a face target were slower following an identical suppressed prime face relative to a suppressed face conveying the same emotional expression but displayed by a different individual. In addition, Almeida et al. (2010) showed that backward-masked primes elicited category- and identity-specific priming both with tool and with animal stimuli, whereas CFS-suppressed primes were associated only with small category-specific priming, and only with tool stimuli.

The foregoing studies relied on an objective measure of conscious perception to ensure that the prime was subliminal (but Izatt et al., 2014 used also a subjective measure). Specifically, using an experimental strategy that has become standard in the study of unconscious processing (Dehaene et al., 1998; Ansorge et al., 2009; Hsieh et al., 2011; Van Opstal et al., 2011) they included experimental trials in which the influence of a subliminal prime on responses to a subsequent target was probed, and prime-awareness test trials in which chance performance at judging the critical property of the prime was demonstrated. Thus, for instance, Almeida et al. (2010) showed that a suppressed prime facilitated response to a categorically congruent target, yet performance at discriminating the category to which this prime belonged was at chance.

It is important to note that with objective measures of conscious perception, it is of tantamount importance to select stimuli that cannot be discriminated above chance: just a few visible trials can jeopardize the success of the whole experiment (e.g., Rouder et al., 2013). Thus, the safest strategy is to select deeply subliminal stimuli at the risk of "overshooting," that is, of cutting into unconscious processing itself. However, the magnitude of such overshooting cannot be assessed because performance is undiscriminably at chance whether the critical stimulus is just under the limen or completely hidden from view (see **Figure 1**). As a consequence, finding that unconscious processing occurs using one method but not using another, may not necessarily reflect that these methods constitutively disrupt different stages of processing: instead, it might simply indicate that the stimulus parameters selected to ensure chance objective performance pushed perceptual processing further from the limen with one method relative to the other.

The objective of the present research was to assess the extent of unconscious processing using liminal stimuli instead of subliminal stimuli. We compared CFS with meta-contrast masking, a method that is thought to interfere with perceptual processing at a relatively late stage (e.g., Del Cul et al., 2007; Enns, 2004) and has been associated with robust priming (e.g., Vorberg et al., 2003; Kentridge et al., 2008; Peremen and Lamy, 2014). We assessed conscious perception of the prime using a sensitive subjective visibility scale akin to the Perceptual Awareness Scale (e.g., Ramsøy and Overgaard, 2004)[1]. One of the main advantages of using this measure in the present context is that it allows using *liminal* stimuli, that is, stimuli that are subjectively invisible on some proportion of the trials and perceived at various degrees of clarity on other trials. In this way, one can prevent conscious processing while minimally encroaching on unconscious processing. In addition to minimizing the distance of the critical stimulus perception from the limen of consciousness, visibility scales allow one to measure this distance – a feature that is particular useful when comparing

---

[1] Subjective measures of conscious perception have been criticized, based on the claim that they may be contaminated by responses biases – a problem that is often referred to as the criterion problem (e.g., Eriksen, 1960; Holender, 1986). However, recent research suggests that using a sensitive subjective measure may circumvent this problem. In a recent study (Peremen and Lamy, 2014) we used meta-contrast masking to manipulate conscious perception of a prime arrow pointing either to the left or to the right and measured conscious perception using a 0-to-3 subjective visibility scale. On trials in which the prime arrow was rated to be completely invisible (rating 0), objective performance at discriminating its direction fell to chance. By contrast, a rating of 1, indicating very faint visibility of the prime, was associated with above-chance performance. Focused scrutiny of the literature reveals that chance forced-choice performance at discriminating a simple feature of a target rendered invisible by a variety of methods, is not uncommon (e.g., Wyart and Tallon-Baudry, 2008; Bahrami et al., 2010). Taken together, these findings suggest that subjective reports of conscious perception can be as sensitive as measures relying on objective discrimination performance.

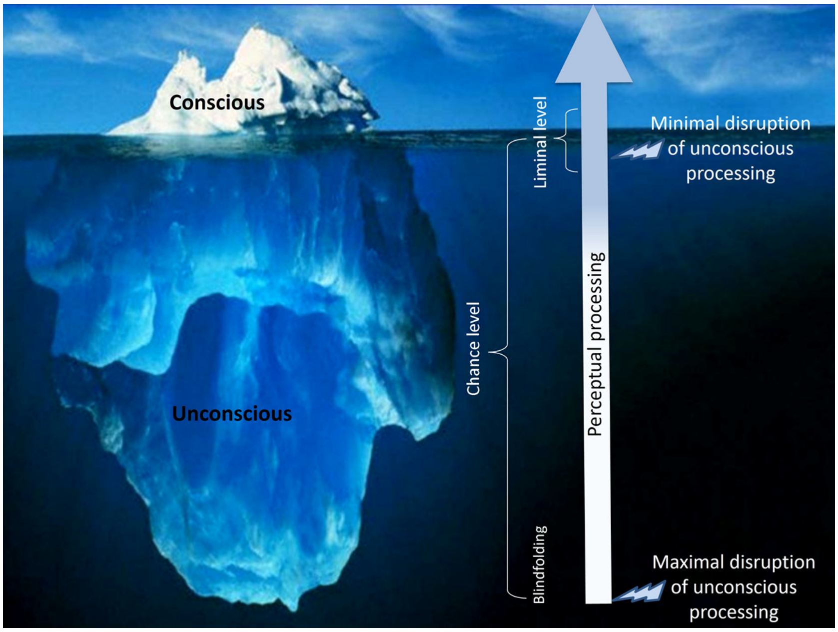


FIGURE 1 | Illustration of the ideas that (1) to maximize sensitivity for measuring unconscious processing, the critical stimulus must be as close as possible to the limen of consciousness and (2) chance performance at discriminating the critical stimulus is not informative with regard to this stimulus' distance from the limen of consciousness.

different methods for preventing conscious perception: similar proportions of invisible trials should indicate similar distances from the limen.

In the present study, we compared the extent of unconscious processing of a prime arrow direction when this arrow was rendered invisible using meta-contrast masking (Experiment 1)[2], or CFS (Experiments 2 and 3). In all three experiments, participants were presented with a liminal prime arrow followed by a clearly visible target arrow, the direction of which was either congruent or incongruent with the prime arrow direction. On each trial, participants first made a speeded forced-choice discrimination response to the direction of the target arrow and then rated the visibility of the prime on a scale ranging from 0 to 3. Unconscious processing of the prime arrow direction was measured as the performance difference between the congruent and incongruent conditions on trials in which participants reported their subjective visibility of the prime to be null.

EXPERIMENT 1

METHODS

Participants

Twenty two right-handed undergraduate students from Tel Aviv University (13 women), age 22–28 years ($M = 24.9$, $SD = 1.9$) were tested in one session for course credit. All subjects reported normal or corrected-to-normal vision.

Apparatus and stimuli

Sample displays are presented in **Figure 2**. The stimuli were presented on a 17-inch 85-Hz CRT monitor. The fixation display consisted of a plus sign (0.2° × 0.2° of visual angle). The prime display consisted of a small arrow (1.6° × 0.8°) and the target-mask display consisted of a larger arrow, 2.1° in width and 1.1° in height. Both arrows were gray (RGB 127, 127, 119) against a black background (RGB 0, 0, 0), were centered at fixation and pointed either leftward or rightward. Thus, the prime arrow either pointed in the same direction as the target arrow (congruent trials) or in the opposite direction (incongruent trials).

Procedure and design

Each trial began with a 500-ms presentation of the fixation display. The prime display then appeared for 24 ms, followed after a variable SOA (0, 24, 47, 71, 94, or 118 ms) by the target-mask display. Then, a blank screen appeared until subjects provided the first response or after 2,000 ms had elapsed, followed by a question mark in the middle of the screen, which prompted the subjects to provide the second response. A new trial began immediately after second response.

On each trial, subjects provided two responses: they first made a speeded response to the target-mask arrow direction by pressing designated keys as fast as possible on the numerical keypad with their right hands ("1" when the arrow pointed to the left and "3" when it pointed to the right). Then, they provided a subjective report of the prime visibility using a scale ranging from 0 ("I saw nothing at all") to 3 ("I saw the arrow clearly") by pressing designated keys ("z," "x," "c," and "v" which were covered with stickers labeled 0, 1, 2, and 3, respectively) on the keyboard with

---

[2] This experiment was reported in a previous paper (Peremen and Lamy, 2014, Experiment 2) to address a different question. Specifically, while in that paper the emphasis was on the comparison between subjective and objective measures of conscious perception, the emphasis here is on the comparison of unconscious processing during meta-contrast masking and continuous flash suppression.

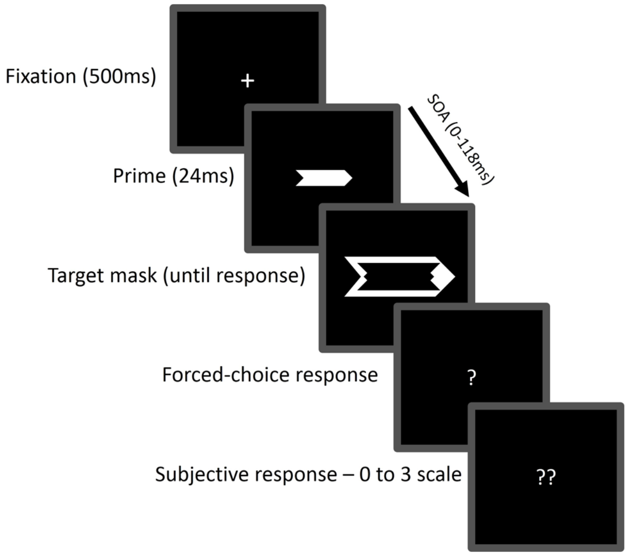


FIGURE 2 | Sequence of events in Experiment 1. In this example, the directions of the prime and target arrows are congruent. Participants were required to make a speeded response to the target mask arrow direction (left or right) and then rate subjective visibility of the prime.

their left hands. Five percent of the trials were catch trials: the target was presented alone, without a prime. The purpose of introducing catch trials was to anchor 0-visibility judgments to situations in which no prime appeared. On 10% of the trials (*no-go* trials) the target arrowheads were truncated and observers had to press the space-bar instead of providing the two responses pertaining to the prime[3]. Each subject completed 500 trials divided into ten blocks and following two practice blocks of 50 trials each. Before practice, the observers viewed the sequence of events at a very slow pace that enabled them to clearly distinguish between the prime and target.

All combinations of the prime and target arrow directions were equiprobable and randomly mixed. They were equally likely to be congruent or incongruent. Prime-to-target SOAs were equiprobable and randomly mixed.

RESULTS

The data from two participants were excluded from analysis: one because his mean RTs were slower than the group's by more than 3 SDs and the other, because of a technical error. Prime-absent (or catch) trials as well as *no-go* trials were excluded from all analyses. In all RT analyses, trials in which responses to the target direction were inaccurate were excluded (2.3%) and so were trials in which the RT exceeded the mean of its cell (resulting from crossing the factors included in the relevant analysis) by more than 2.5 SDs (fewer than 1% of the trials). An ANOVA with SOA as a within-subject factor and mean visibility as the dependent measure revealed that mean visibility followed the U-shaped pattern characteristic of type-B meta-contrast masking (Kolers and Rosner, 1960) and was lowest at the 47-ms SOA (this trend did not reach significance after Huynh–Feldt correction, $F(5,75) = 2.69$, $p < 0.09$). The mean proportion of trials per visibility for each SOA is shown in **Figure 3**[4].

Reaction times

A linear mixed-effects model with visibility (0, 1, 2, or 3) and congruency (congruent vs. incongruent) as within-subject factors was performed on the mean RTs. Mean RT and accuracy data are presented in **Table 1** and the mean congruency effect at each visibility level is shown in **Figure 4**[5]. The main effect of congruency was significant, $F(1,19) = 86.94$, $p < 0.0001$, with faster RTs when the prime and target arrows were congruent than when they were incongruent. The main effect of visibility was also significant, $F(3,53) = 32.16$, $p < 0.0001$, with longer RTs as visibility increased. The interaction between the two factors was significant, $F(3,53) = 3.7$, $p < 0.02$. Further analyses revealed that the congruency effect was larger for visibility three than for all other levels, all $ps > 0.03$ and that the congruency effects for visibility levels 0, 1, and 2 did not differ from each other, all $Fs < 1$. Crucially, the congruency effect was significant when visibility was null, 49 ms $F(1,53) = 14.82$, $p < 0.001$.

Accuracy

Similar analyses were conducted on the accuracy data pertaining to the responses to the target arrow. They showed similar trends, thus ensuring that speed-accuracy trade-off was not a concern. The main effect of visibility was significant, $F(3,53) = 6.81$, $p < 0.001$, the main effect of congruency approached significance $F(1,19) = 3.75$, $p < 0.07$ and the interaction between the two factors was not significant, $F < 1$.

EXPERIMENT 2

METHODS

Participants

Fifteen undergraduate students from Tel Aviv University (fourteen right-handed, 11 women,), age 20–27 years ($M = 23$, SD = 1.65) were tested in one session for course credit. All subjects reported normal or corrected-to-normal vision.

Apparatus, stimuli, procedure, and design

The apparatus was the same as in Experiment 1 except for the following changes. All stimuli were presented on a LCD monitor (SyncMaster) with 1920 × 1080 resolution, 120 Hz refresh rate

---

[3] The use of a go no-go task is related to the goals of Peremen and Lamy (2014) study and is irrelevant here. It will therefore not be considered further.

[4] The distribution of visibility ratings could considerably vary between observers. However, we chose not to exclude subjects based on considerations of balanced visibility rating distribution. Instead, in order to overcome the distortions that might result from unbalanced repeated measures data, we used a mixed effects model to analyze the data when visibility was as a factor. Importantly, however, for this and the following experiments, the results remained the same when subjects with unbalanced distributions (fewer than 10% or more than 65% of 0-visibility trials) were excluded.

[5] The relatively high mean RT in this and the next experiments (>600 ms) are likely to result from the dual-task situation. Consistent with this conjecture, we recently showed that when subjects had to respond to both the target and prime (as in the present experiments), RTs were on the order of 650 ms, whereas when they had to respond only to the target (all other things being identical), their RTs fell below 400 ms (Peremen and Lamy, 2014).

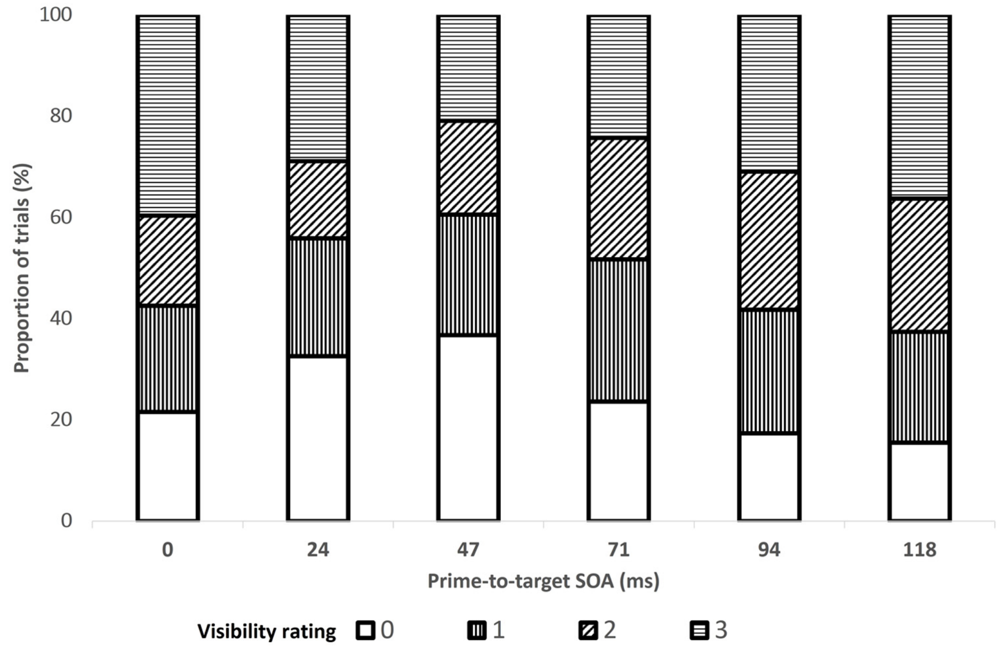


FIGURE 3 | Proportion of trials in each level of prime visibility (0–3) as a function of the SOA between the prime and target, in Experiment 1.

Table 1 | Mean reaction times and accuracy on congruent and on incongruent trials in Experiment 1 as a function of visibility rating.

	Reaction times (ms)		Accuracy (%)	
Visibility	**Congruent**	**Incongruent**	**Congruent**	**Incongruent**
0	606.2	655.6	98.7	97.8
1	640.9	683.8	99.0	98.2
2	693.7	746.2	98.0	98.2
3	653.5	747.3	97.0	95.9

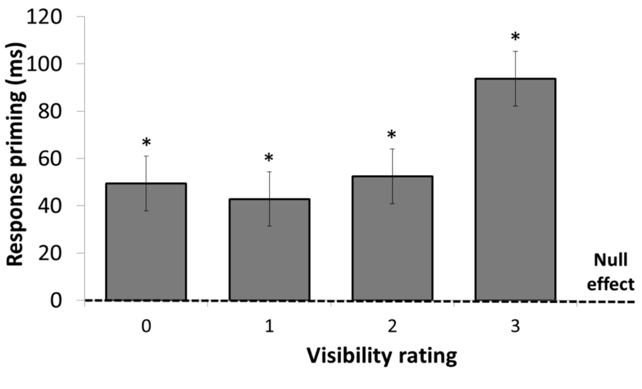


FIGURE 4 | Mean response-priming effect in milliseconds in Experiment 1, as a function of visibility rating. Priming was significant for visibility 0–3. Error bars represent standard errors. $*p < 0.002$.

controlled by a Power Samsung 3D PC. In order to create stereoscopic perception the stimuli were viewed through SSG-M3150GB 3D Active Glasses (battery powered), which let one image through the left eye while blocking stimulation to the right eye and another image to the right eye while blocking stimulation to the left eye, with a 60-Hz alternation rhythm that is beyond the perceptual threshold. The target display was presented together with the Mondrian suppressors to one eye, whereas the prime display was displayed to the other ("suppressed") eye.

Sample displays are presented in **Figure 5**. The prime display consisted of two filled horizontal arrows (1.72° × 0.46° each) pointing in the same direction, either left or right, and presented 0.57° above and below the center of the screen. The two prime arrows were gray and appeared at variable contrast levels of 20, 60, or 100% of maximum contrast level (RGB 195, 195, 195). The target display consisted of a horizontal white outline arrow (1.72°× 0.57°) pointing either leftward or rightward. All arrows were presented against a black background. The suppressors were Mondrians, that is, randomly colored figures of partly overlapping rectangles of varying sizes and colors. A white rectangular frame (18.16° × 18.16°) centered at fixation was presented to each eye throughout the trial.

Each trial began with a 1,000-ms presentation of the fixation display. The prime display was then faded in by ramping up its contrast from 0% to a contrast level of 20, 60, or 100% in 200 ms. It remained on the screen until the target was presented, following a variable SOA (250, 350, 450, 550, or 650 ms). The target display remained visible until response. The subsequent events as well as the response requirements were the same as in Experiment 1.

The two prime arrows and the target arrow were equally likely to point to the left or right, and were therefore equally likely to be

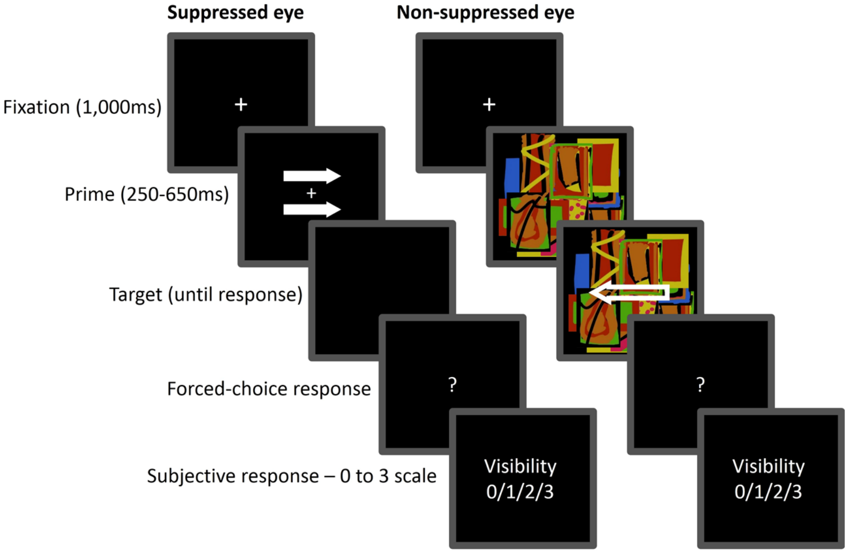


FIGURE 5 | Sequence of events in Experiment 2. The prime arrows were gradually introduced and presented to one eye (suppressed eye), while the target was superimposed on a dynamic Mondrian and presented to the other eye (non-suppressed eye). Here, the directions of the prime and target arrows are incongruent. Participants were required to make a speeded response to the target arrow direction (left or right) and then rate subjective visibility of the prime.

congruent or incongruent. Conditions of prime-arrows direction, target-arrow direction, SOA and prime contrast were randomly mixed.

RESULTS

In all RT analyses, trials in which responses to the target arrow direction were inaccurate were excluded (1.2%) and so were trials in which the RT exceeded the mean of its cell by more than 2.5 SDs (fewer than 1.6% of the trials).

An ANOVA with SOA and prime-contrast level as within-subject factors and mean visibility as the dependent variable revealed significant main effects, $F(4,56) = 18.51$, $p < 0.0001$ and $F(2,28) = 17.16$, $p < 0.0001$, respectively, with higher visibility as the SOA and prime-contrast increased. The significant interaction between these factors, $F(8,112) = 4.87$, $p < 0.002$ indicated that the effect of prime contrast became significant only for SOAs exceeding 350 ms. The mean proportions of trials per visibility is shown in **Figure 6** as a function of SOA and in **Figure 7** as a function of prime-contrast level.

Reaction times

A linear mixed-effects model with visibility (0, 1, 2, or 3), congruency (congruent vs. incongruent), prime-contrast level (20, 60, 100%) and SOA (250, 350, 450, 550, or 650 ms) as within-subject factors was performed on the mean RTs of correct trials. The main effect of SOA was significant, $F(4,56) = 22.95$, $p < 0.0001$ with slower RTs as SOA increased and did not interact with congruency, $F < 1$. There was no significant effect of prime contrast $\mathrm{F}(2,28) = 1.99$, $p = 0.16$, and no interaction involving this factors, all Fs < 1. Mean RTs and accuracy data are presented in **Table 2** and the mean congruency effect at each visibility level is shown in **Figure 8**. The main effect of congruency was significant, $F(1,14) = 41.39$, $p < 0.0001$ with faster RTs when the directions of the prime and target arrows were congruent than when they were incongruent. The main effect of visibility was also significant, $F(3,40) = 104.28$, $p < 0.0001$, indicating that RTs were slower for 0- than for 1-, 2- and 3-visibility trials, all ps < 0.0002. There was a significant interaction between the two factors, $F(3,38) = 8.04$, $p < 0.0003$. Further analyses revealed that the congruency effect was significant for visibility levels 1, 2 and 3, $F(1,38) = 5.06$, $p < 0.03$, $F(1,38) = 12.6$, $p < 0.001$ and $F(1,38) = 45.12$, $p < 0.001$, respectively but crucially and unlike the pattern of results observed in Experiment 1, response priming was not significant when visibility was null, $F < 1$. As is clear from **Figure 8** response priming increased linearly with increasing levels of visibility.

Accuracy

Similar analyses conducted on the accuracy data showed similar trends. The main effect of visibility was significant, $F(3,37) = 3.82$, $p < 0.02$. No effect involving congruency approached significance, all ps > 0.2.

DISCUSSION

The results of Experiments 1 and 2 revealed a markedly different pattern. When the prime was invisible, response priming was significant when invisibility was achieved using meta-contrast masking (Experiment 1), but was absent when invisibility was achieved using CFS (Experiment 2). These findings suggest that CFS interferes with processing more deeply than does meta-contrast masking. However, four alternative accounts must be considered.

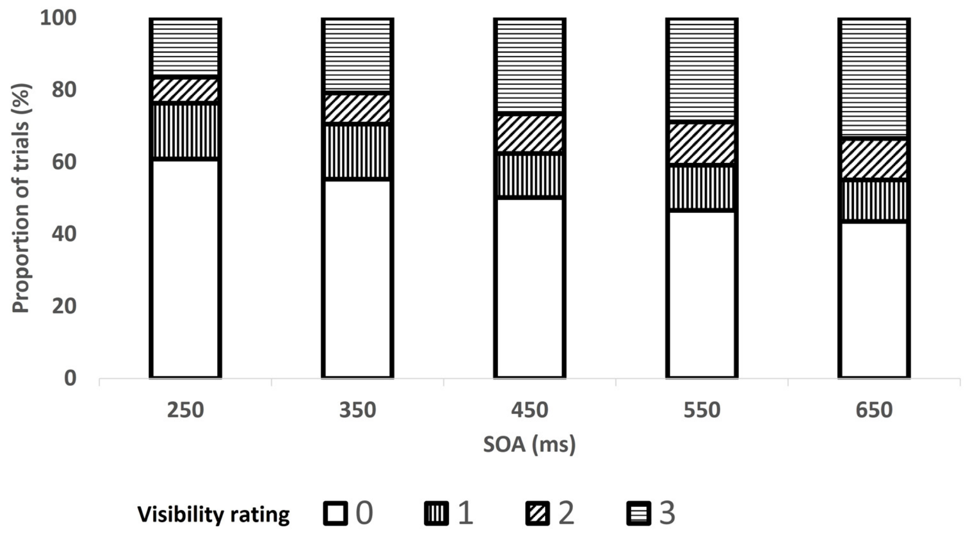


FIGURE 6 | Proportion of trials in each level of prime visibility (0–3) as a function of the SOA between the prime and target, in Experiment 2.

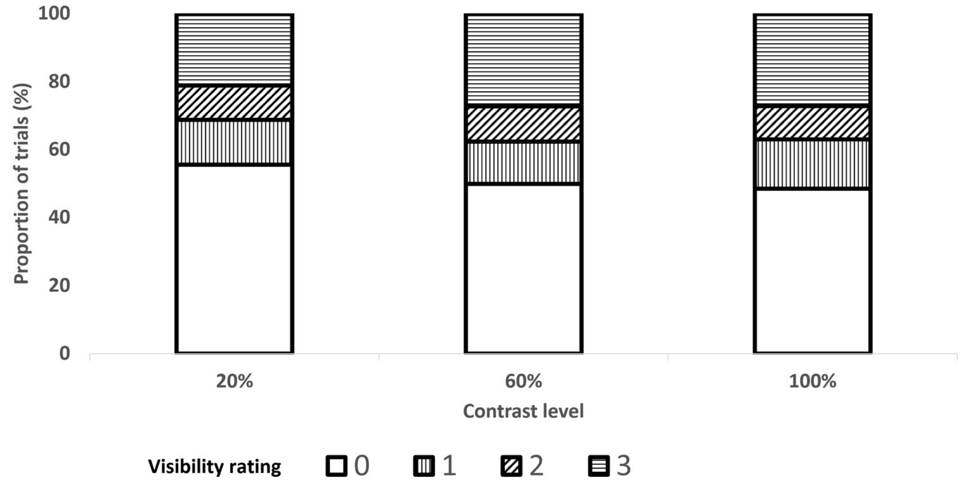


FIGURE 7 | Proportion of trials in each level of prime visibility (0–3) as a function of prime contrast level, in Experiment 2.

Table 2 | Mean reaction times and accuracy on congruent and on incongruent trials in Experiment 2 as a function of visibility rating.

	Reaction times (ms)		Accuracy (%)	
Visibility	**Congruent**	**Incongruent**	**Congruent**	**Incongruent**
0	685.5	689.3	99.5	99.0
1	757.1	779.5	99.0	97.7
2	750.4	791.1	99.5	96.4
3	697.7	746.5	99.2	97.9

First, although the stimuli used were largely similar in the two experiments, they differed in a few respects. For instance, the prime was one central arrow in Experiment 1 and two eccentric (albeit foveal) arrows in Experiment 2. Although stimulus-related differences should not matter as long as the primes are liminal to the same extent, one could claim that there might be qualitative differences in unconscious processing of central and eccentric stimuli.

Second, when the prime was clearly visible (visibility 3), response priming was larger in the meta-contrast than in the CFS experiment (93 vs. 49 ms, respectively). Thus, it may be the case that the meta-contrast masking paradigm yielded larger response priming overall in our experiment and was therefore more sensitive for detecting unconscious processing than was the CFS paradigm. In order to test this possibility, we analyzed the data from participants who showed the *largest* response priming effects for maximum visibility in the CFS experiment (i.e., with response priming exceeding the median effect of the group, 57 ms). The

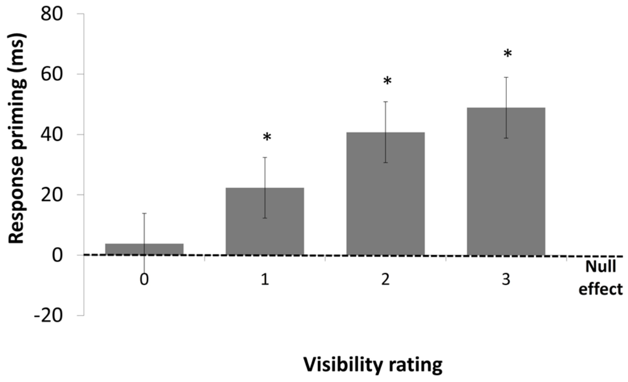


FIGURE 8 | Mean response-priming effect in milliseconds in Experiment 2, as a function of visibility rating. Priming was significant for visibility 1, 2, and 3, but not when visibility was null. Error bars represent standard errors. *$p < 0.03$.

mean congruency effect for visibility-3 trials in large-response-priming participants was 78 ms, and was therefore similar to the mean congruency effect in Experiment 1 (93 ms). Yet, response priming when the prime was invisible remained null (4 ms, $F < 1$). Conversely, we analyzed the data from participants who showed the *smallest* response priming effects for maximum visibility in the meta-contrast masking experiment (i.e., response priming effect lower than the median effect of the group, 75 ms). The mean congruency effect for visibility-3 trials in small-response-priming participants was 54 ms, and was therefore similar to the mean congruency effect in Experiment 2 (49 ms). Yet, in line with our prediction, response priming was still highly significant when the prime was invisible [75 ms, $F(1,23) = 21.86$, $p < 0.0001$]. We can thus conclude that differences in the magnitudes of response priming on high-visibility trials does not account for the observed differences in unconscious processing between the two methods.

Third, as the distribution of trials across visibility levels varied as a function of SOA (**Figure 6**) and prime contrast (**Figure 7**), our finding of a large congruency effect when the prime was visible (ratings 1, 2, and 3) but not when it was invisible (rating 0) may reflect SOA- or prime-contrast- rather than visibility-related differences. In other words, the null response priming effect on 0-visibility trials may mainly emanate from short-SOA or low-prime-contrast trials, whereas the large response priming effect on visibility-3 trials may mainly emanate from long-SOA or high-prime-contrast trials (note that this problem does not apply to Experiment 1 because priming was found for visibility 0). The fact that the congruency effect interacted with neither SOA nor contrast level is inconsistent with such a claim, yet we nevertheless conducted additional analyses to examine this possibility. We focused only on the SOA (250 ms) and prime-contrast level (20%) for which visibility three ratings were least frequent. The congruency effect was still present for visibility-3 trials, $F(1,32) = 3.58$, $p < 0.07$ and $F(1,32) = 4.93$, $p < 0.04$, for the 250-ms SOA and 20%- prime contrast, respectively, and still absent for visibility-0 trials, both Fs < 1.

The fourth alternative account rests on the observation that the proportion of 0-visibility trials was overall larger in the CFS than in the meta-contrast experiment. The lowest proportion of such trials was 44% (with the 650-ms SOA) in the former, whereas the highest proportion in the latter experiment was 37% (with the 47-ms SOA). As explained in the introduction, such a state of affairs indicates that the prime stimuli were further from the limen of consciousness in the CFS than in the meta-contrast experiment, which could explain why we failed to observe unconscious processing with CFS.

Although the additional analyses reported above provide a partial answer to the second and third issues, the objective of Experiment 3 was to address all four issues more directly.

EXPERIMENT 3

In this experiment, we again used CFS to manipulate conscious perception of the prime but introduced three changes in order to test our conclusions from Experiment 2 against alternative accounts. First, the prime and target arrows were now identical to those used in Experiment 1, so as to preclude any account based on stimulus-based differences between the meta-contrast and CFS experiments. Second, to ensure that the unconscious and conscious conditions were physically identical, we used only one contrast level and one prime-target SOA. Third, we selected a high prime-contrast level and ramped it up faster than in Experiment 2 in order to bring the prime stimulus to a closer distance to the limen. Specifically, we aimed at obtaining a percentage of 0-visibility trials similar or smaller than for the SOA associated with the highest such percentage in the meta-contrast experiment (47 ms), in which a significant priming effect was observed.

Note that while we physically equated the prime and target stimuli in Experiments 3 and 1, we used different SOAs (from 0 to 118 ms in Experiment vs. 200 ms in Experiment 3). Obviously, stimulus conditions to prevent consciousness are going to be different in any two methods, in order for these methods to be distinguished: had we used exactly the same stimuli and SOAs in the CFS as in the meta-contrast experiments, prime stimuli would have suffered from both meta-contrast masking and CFS. Consistent with this observation, it is noteworthy than none of the previous studies which compared CFS and backward masking used identical stimuli or temporal parameters. For instance, Faivre et al. (2012) presented the critical primes for 2,500 ms with CFS and for 50 ms with backward masking. Likewise, Almeida et al. (2010) presented their primes twice for 100 ms in the CFS condition and once for 35 ms in the backward masking condition. However, in Experiment 3, in order to minimize the potential consequences of using long prime durations with CFS, we selected a relatively short SOA, namely, 200 ms, which ensured that no meta-contrast masking could occur (e.g., Enns, 2004). If the findings of Experiment 2 resulted from genuine differences between CFS and meta-contrast masking rather than from any of the four alternative accounts we suggested then we should expect to replicate these findings in the present experiment.

METHODS

Participants

Thirteen undergraduate students from Tel Aviv University (12 right-handed, eight women), age 20–28 years ($M = 24.0$, SD $= 2.4$)

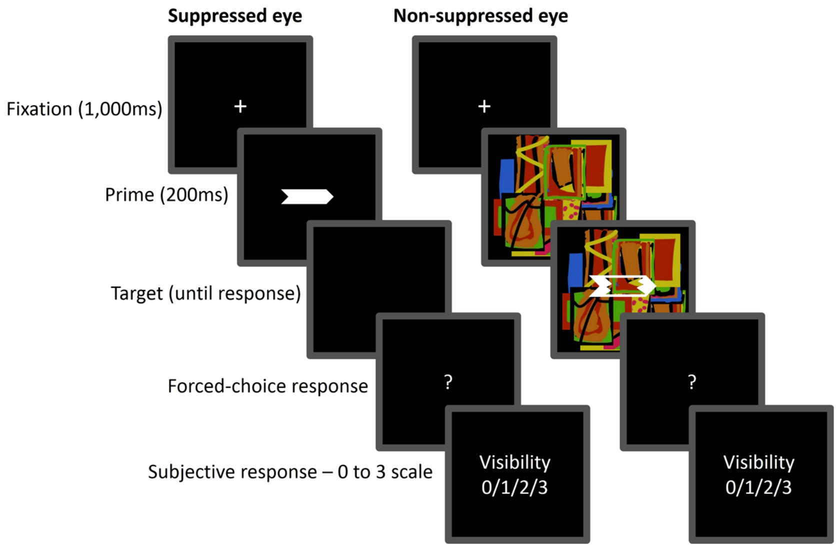


FIGURE 9 | Sequence of events in Experiment 3. Prime-to-target SOA was fixed at 200 ms and prime contrast level also fixed.

were tested in one session for course credit or for a 30-NIS pay (~8USD). All subjects reported normal or corrected-to-normal vision.

Apparatus, stimuli, procedure, and design

The apparatus, stimuli, procedure and design were the same as in Experiment 2 except for the following changes. First, the prime and mask arrows were exactly the same as in Experiment 1. Sample displays are presented in **Figure 9**. Second, prime contrast was not manipulated: on each trial, the prime display was faded in by ramping up its contrast to 100% of maximum contrast level in 50 ms. Finally, the target display followed the prime after a fixed SOA of 200 ms.

RESULTS AND DISCUSSION

The data from one participant was excluded from analysis because upon debriefing, he reported using the strategy of foveating the periphery of the display, which helped him perceive the prime more easily. Prime-absent (or catch) trials as well as *no-go* trials were excluded from all analyses. In all RT analyses, trials in which responses to the target arrow direction were inaccurate were excluded (1.9%) and so were trials in which the RT exceeded the mean of its cell by more than 2.5 SDs (fewer than 2.4% of the trials). The mean proportions of trials per visibility are shown in **Figure 10**.

Reaction times

A linear mixed-effects model with visibility (0, 1, 2, or 3) and prime-target congruency (congruent vs. incongruent) as within-subject factors was performed on the mean RTs of correct trials. Mean RTs are presented in **Table 3** and the mean congruency effect at each visibility level is shown in **Figure 11**. The main effect of congruency was significant, $F(1,11) = 159.26$, $p < 0.0001$, with faster RTs when the directions of the prime and target arrows were congruent than when they were incongruent. The main effect of visibility was also significant, $F(3,33) = 12.83$, $p < 0.0001$, indicating that RTs became slower as mean visibility ratings increased. There was a significant interaction between the two factors, $F(3,32) = 24.74$, $p < 0.0001$. Closely replicating the findings of Experiment 2, the congruency effect increased as visibility

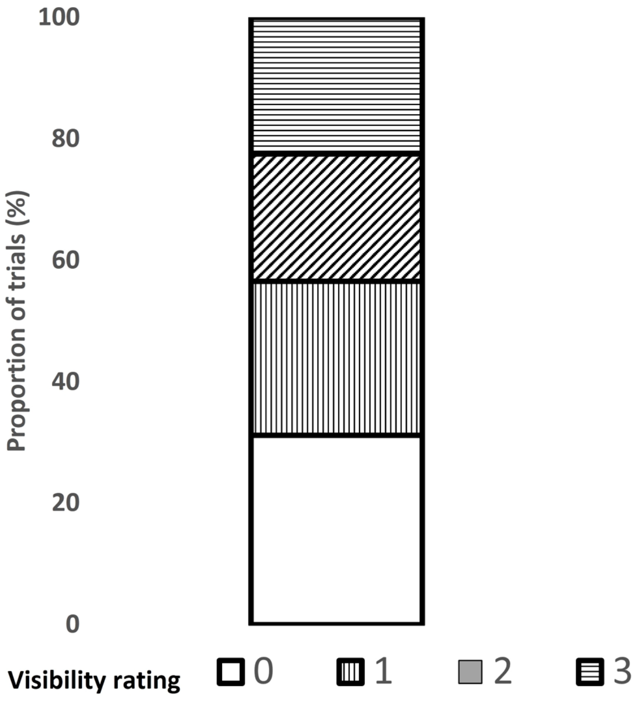


FIGURE 10 | Proportion of trials for each level of prime visibility (0–3) in Experiment 3.

Table 3 | Mean reaction times and accuracy on congruent and on incongruent trials in Experiment 3 as a function of visibility rating.

	Reaction times (ms)		Accuracy (%)	
Visibility	Congruent	Incongruent	Congruent	Incongruent
0	669.3	675.2	99.1	98.8
1	653.2	689.8	99.3	98.9
2	672.8	712.0	99.2	99.0
3	654.2	736.6	98.8	98.2

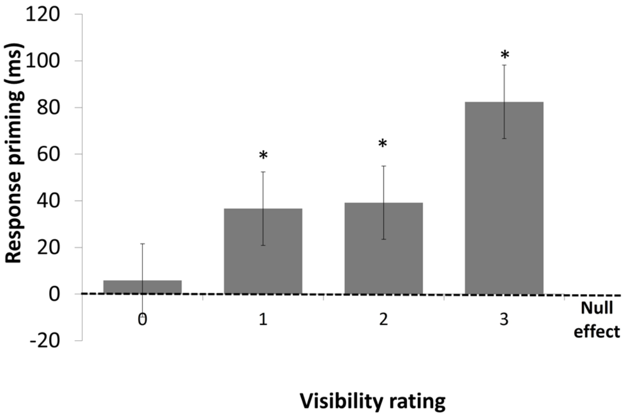


FIGURE 11 | Mean response-priming effect in milliseconds in Experiment 3, as a function of visibility rating. Priming was significant for visibility 1, 2, and 3, but not when visibility was null. Error bars represent standard errors. *$p < 0.001$.

increased and was significant for visibility levels 1, 2, and 3, $F(1,32) = 33.0$, $p < 0.001$, $F(1,32) = 31.19$, $p < 0.001$, and $F(1,32) = 147.74$, $p < 0.001$, respectively. Crucially, however, it was again non significant when visibility was null, $F = 1.03$, $p = 0.32$.

Accuracy

Similar analyses were conducted on the accuracy data. The congruency effect was not significant, $F(1,11) = 2.25$, $p = 0.16$ and neither were all other effects, all *F*s < 1.

The results replicated the findings of Experiment 2, yet they can be accounted for by none of alternative interpretations raised with respect to Experiment 2. In particular, the magnitude of response priming on maximum-visibility trials was similar to the one observed with meta-contrast masking (Experiment 1). In addition, the proportion of null-visibility trials was smaller in this experiment than in Experiment 2 and was now similar to the proportion observed in the meta-contrast experiment. In fact, this proportion was smaller here (31.2%) than with the 24 and 47-ms SOAs (32.6 and 36.7%, respectively), for which significant response priming was observed in Experiment 1. Thus, the stimuli were unlikely to be further from the limen of consciousness in the CFS relative to the meta-contrast experiment.

GENERAL DISCUSSION

In this study, we compared unconscious processing under meta-contrast masking and CFS. Conscious perception was assessed using a sensitive visibility scale ranging from 0 to 3 and unconscious processing was measured as a significant effect of the congruency between the directions of a prime and target arrows when participants reported not seeing the prime at all (i.e., when its visibility was rated to be 0). The central finding is that unconscious processing was substantial with meta-contrast masking but absent with CFS.

Although previous studies have also compared different suppression methods and shown that CFS allows only little unconscious processing, it is important to report conceptual replications of these findings on the backdrop of the increasing popularity of CFS as a tool to study unconscious processing. We extend previous findings by comparing CFS to meta-contrast masking rather than pattern backward masking or gaze-contingent crowding, and by probing unconscious response priming that relies on simple shape perception, rather than semantic category discrimination or emotional processing (Almeida et al., 2010 and Faivre et al., 2012, respectively). In addition, our comparison involved exactly the same prime and target stimuli unlike Almeida et al. (2010) who added 70% of noise to the prime stimuli in the masking but not in the CFS experiment and Faivre et al. (2012) study who cropped peripheral facial attributes (e.g., hair, ears) in the masking but not in the CFS experiment. Finally and most importantly, we used a novel methodology to ensure that the critical stimuli were at a comparable distance from the limen of consciousness during CFS and meta-contrast masking.

COMPARISON WITH PREVIOUS CFS STUDIES

The finding that CFS disrupts relatively low-level perceptual processes calls for a reappraisal of previous demonstrations that highly complex processing can be performed when conscious perception of the critical stimuli is prevented using CFS. Therefore, our study accredits the notion that unconscious processing demonstrated by measuring the time of breaking of CFS suppression (e.g., Jiang et al., 2006; Costello et al., 2009; Mudrik et al., 2011; Sklar et al., 2012; Lupyan and Ward, 2013) resulted from partial awareness of the suppressed stimuli (e.g., Stein et al., 2011; Gayet et al., 2014). However, our results appear to be at odds with previous reports of unconscious priming during CFS.

Bahrami et al. (2010) examined whether invisible numerical stimuli could prime a visible numerical target. They measured subjective awareness on a scale ranging from 0 to 2 on each trial and reported a significant effect of the numerical distance between the prime and target on 0-prime-visibility trials. However, unconscious numerical processing was very tenuous. The priming effect, measured as the RT-difference between prime-present and prime-absent trials, was found to depend on the identity of the prime only for one specific prime-target distance: RTs were faster for same than for different prime-target trials only for the prime-target distance of -2 (and not for distances of -1, 1, and 2).

Almeida et al. (2010) reported a small (<15 ms), yet significant category-specific priming effect for tool vs. animal stimuli with invisible primes. CFS-suppressed stimuli were held to be invisible based on an awareness pre-test which determined the individual stimulus contrast for which participants were at chance at discriminating the prime category. This stimulus contrast was used in the main experiment. Two aspects of this procedure, however, suggest that partial awareness may have occurred. First, the awareness-check block was run before the experimental trials, so that participants were more practiced for trials in which priming was measured than for trials in which conscious perception was assessed. As perception of the prime is likely to increase with practice (e.g., Schwiedrzik et al., 2009), partial awareness of the prime cannot be excluded. In addition, the authors adopted a rather lenient criterion for consciousness: forced-choice discrimination performance ranging between 35 and 65% was held to reflect chance performance.

Faivre et al. (2012) reported unconscious priming elicited by CFS-suppressed faces. A significant improvement over previous study is that priming and conscious perception were measured under exactly the same conditions. The finding of Faivre et al.'s (2012) study is not necessarily incompatible with our results, however. While we found no priming for prime and target arrows that were physically different from each other, Faivre et al. (2012) reported priming in the form of a performance cost when the prime and target were identical, suggesting that sensory adaptation may have occurred. By contrast, they found that the same faces did not bias affective judgments of a subsequent neutral target. Taken together, these findings suggest that CFS suppression may allow very low-level perceptual processing of the prime but not response priming. Further research is required to further test this hypothesis.

Finally, Izatt et al. (2014) provided only weak evidence of unconscious priming by CFS-suppressed faces. First, their stimuli were considered to be invisible when subjects reported either no experience or a brief glimpse of the stimulus, that is, in conditions that are equivalent to visibility levels 0 and 1 of the present study. Considering that we found unconscious priming to be significant for visibility 1 (but not for null visibility), any unconscious priming demonstrated when these two visibility levels are collapsed may have resulted from partial awareness. Second, one could infer that unconscious priming occurred during CFS only from the fact that unconscious priming was significant across masking conditions (backward masking and CFS) and did not interact with masking technique. Thus, there was no direct test of unconscious priming by CFS-suppressed stimuli.

METHODOLOGICAL IMPLICATIONS FOR THE STUDY OF UNCONSCIOUS PROCESSING

Our findings show that in the search for the boundaries of unconscious processing, the method used to prevent conscious perception matters: failure to observe that some process can be performed without conscious perception with one method does not necessarily entail that conscious perception is necessary for this process. In the present study, for instance, identification of the prime shape and activation of the motor response associated with this shape were found to be largely independent of conscious perception: priming was of the same magnitude when the prime was subjectively invisible, barely visible or almost clearly visible (although priming was further boosted when visibility was maximal). Yet, had one relied on the findings resulting from preventing conscious perception using CFS, the conclusion would have been that shape processing and/or motor preparation require conscious perception.

It follows that the best-suited methods to study unconscious processing are those that can entirely prevent conscious perception while minimally disrupting unconscious processing. In order to uncover such methods, different means of suppressing conscious vision must be compared. We suggest that such comparison is possible only if one ensures that the critical stimuli are equally close to the limen of consciousness for each of the compared methods. (Here, we defined conscious perception at the most basic level, namely, with regard to perception of the critical stimulus' mere presence rather than with regard to perception of one of its features). We further suggest that a fruitful approach to measure distance from the limen is to use stimulus and temporal parameters that are associated with liminal perception and to assess conscious perception using a sensitive subjective scale. In this way, the distance from the limen can be estimated as the percentage of 0-visibility trials[6]. Again, it should be noted that objective measures of conscious perception cannot provide an estimate of such distance, as explained in the introduction. Here, we showed that although stimuli rendered invisible using CFS and meta-contrast masking (Experiment 1 vs. 3) were equally distant from the limen and produced similar priming effects for maximum visibility trials, unconscious response priming was large with one method and absent with the other.

ACKNOWLEDGMENTS

Support was provided by the Israel Science Foundation (ISF) Grant No. 1475/12 and the Binational Science Foundation (BSF) Grant No. 2009425 to Dominique Lamy. We thank Yael Green, Anya Kolgov, Adam Krashniak, Nir Shalev, Alon Zivony and Or Yaniv, for their help in running the experiments.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fpsyg.2014.00969/abstract

REFERENCES

Almeida, J., Mahon, B. Z., and Caramazza, A. (2010). The role of the dorsal visual processing stream in tool identification. *Psychol. Sci.* 21, 772–778. doi: 10.1177/0956797610371343

---

[6] One could argue that the criterion used when reporting visibility of the prime may have been more conservative in the meta-contrast masking than in the CFS experiment. In other words, participants may have reported 0 visibility despite partial awareness of the prime in the former but not in the latter experiment. However, the findings of Peremen and Lamy (2014) study clearly argue against this claim. Using exactly the same stimuli and SOAs as in Experiment 1, we showed that participants were at chance at discriminating the direction of the prime arrow when reporting 0 visibility: had meta-contrast masking induced a conservative criterion, performance should have been above chance.

Almeida, J., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proc. Natl. Acad. Sci. U.S.A.* 105, 15214–15218. doi: 10.1073/pnas.0805867105

Ansorge, U., Kiss, M., and Eimer, M. (2009). Goal-driven attentional capture by invisible colors: evidence from event-related potentials. *Psychon. Bull. Rev.* 16, 648–653. doi: 10.3758/PBR.16.4.648

Bahrami, B., Petra, V., Eva, S., Silvia, P., Brian, B., and Geraint, R. (2010). Unconscious numerical priming despite interocular suppression. *Psychol. Sci.* 21, 2, 224–233. doi: 10.1177/0956797609360664

Breitmeyer, B. (1978). Meta-contrast masking as a function of mask energy. *Bull. Psychon. Soc.* 12, 50–52. doi: 10.3758/BF03329621

Breitmeyer, B. G., and Ganz, L. (1976). Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. *Psychol. Rev.* 83, 1–36. doi: 10.1037/0033-295X.83.1.1

Costello, P., Jiang, Y., Baartman, B., McGlennen, K., and He, S. (2009). Semantic and subword priming during binocular suppression. *Conscious. Cogn.* 18, 375–382. doi: 10.1016/j.concog.2009.02.003

Dehaene, S., Naccache, L., Le Clec'H, G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., et al. (1998). Imaging unconscious semantic priming. *Nature* 395, 597–600. doi: 10.1038/26967

Del Cul, A., Baillet, S., and Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biol.* 5:e260. doi: 10.1371/journal.pbio.0050260

Di Lollo, V., Enns, J. T., and Rensink, R. A. (2000). Competition for consciousness among visual events: the psychophysics of reentrant visual processes. *J. Exp. Psychol. Gen.* 129, 481. doi: 10.1037/0096-3445.129.4.481

Enns, J. T. (2004). Object substitution and its relation to other forms of visual masking. *Vision Res.* 44, 1321–1331. doi: 10.1016/j.visres.2003.10.024

Erdelyi, M. H. (1986). Experimental indeterminacies in the dissociation paradigm of subliminal perception. *Behav. Brain Sci.* 9, 30–31. doi: 10.1017/S0140525X00021348

Erdelyi, M. H. (2004). Subliminal perception and its cognates: theory, indeterminacy, and time. *Conscious. Cogn.* 13, 73–91. doi: 10.1016/S1053-8100(03)00051-5

Eriksen, C. W. (1960). Discrimination and learning without awareness: a methodological survey and evaluation. *Psychol. Rev.* 67, 279–300. doi: 10.1037/h0041622

Faivre, N., Berthet, V., and Kouider, S. (2012). Nonconscious influences from emotional faces: a comparison of visual crowding, masking, and continuous flash suppression. *Front. Psychol.* 3:129. doi: 10.3389/fpsyg.2012.00129

Faivre, N., Berthet, V., and Kouider, S. (2014). Sustained invisibility through crowding and continuous flash suppression: a comparative review. *Front. Psychol.* 5:475. doi: 10.3389/fpsyg.2014.00475

Fang, F., and He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nat. Neurosci.* 8, 1380–1385. doi: 10.1038/nn1537

Fogelson, S. V., Kohler, P. J., Miller, K. J., Granger, R., and Tse, P. U. (2014). Unconscious neural processing differs with method used to render stimuli invisible. *Front. Psychol.* 5:601. doi: 10.3389/fpsyg.2014.00601

Gayet, S., Van der Stigchel, S., and Paffen, C. L. (2014). Breaking continuous flash suppression: competing for consciousness on the pre-semantic battlefield. *Front. Psychol.* 5:460. doi: 10.3389/fpsyg.2014.00460

Greenwald, A., Draine, S., and Abrams, R. (1996). Three cognitive markers of unconscious semantic activation. *Science* 237, 1699–1701. doi: 10.1126/science.273.5282.1699

Hesselmann, G., and Malach, R. (2011). The link between fMRI-BOLD activation and perceptual awareness is "stream-invariant" in the human visual system. *Cereb. Cortex* 21, 2829–2837. doi: 10.1093/cercor/bhr085

Holender, D. (1986). Semantic activation without conscious identification in dichotic listening, parafoveal vision, and visual masking: a survey and appraisal. *Behav. Brain Sci.* 9, 1–23. doi: 10.1017/S0140525X00021269

Hsieh, P. J., Colas, J. T., and Kanwisher, N. (2011). Pop-out without awareness: unseen feature singletons capture attention only when top-down attention is available. *Psychol. Sci.* 22, 1220–1226. doi: 10.1177/0956797611419302

Izatt, G., Dubois, J., Faivre, N., and Koch, C. (2014). A direct comparison of unconscious face processing under masking and interocular suppression. *Front. Psychol.* 5:659. doi: 10.3389/fpsyg.2014.00659

Jiang, Y., Costello, P., Fang, F., Huang, M., and He, S. (2006). A gender- and sexual orientation-dependent spatial attentional effect of invisible images. *Proc. Natl. Acad. Sci. U.S.A.* 103, 17048–17052. doi: 10.1073/pnas.0605678103

Kanai, R., Walsh, V., and Tseng, C. H. (2010). Subjective discriminability of invisibility: a framework for distinguishing perceptual and attentional failures of awareness. *Conscious. Cogn.* 19, 1045–1057. doi: 10.1016/j.concog.2010.06.003

Kang, M. S., Blake, R., and Woodman, G. F. (2011). Semantic analysis does not occur in the absence of awareness induced by interocular suppression. *J. Neurosci.* 31, 13535–13545. doi: 10.1523/JNEUROSCI.1691-11.2011

Kentridge, R. W., Nijboer, T. C., and Heywood, C. (2008). Attended but unseen: visual attention is not sufficient for visual awareness. *Neuropsychologia* 46, 864–869. doi: 10.1016/j.neuropsychologia.2007.11.036

Kim, C. Y., and Blake, R. (2005). Psychophysical magic: rendering the visible 'invisible'. *Trends Cogn. Sci.* 9, 381–388. doi: 10.1016/j.tics.2005.06.012

Kolers, P. A., and Rosner, B. S. (1960). On visual masking (metacontrast): dichoptic observation. *Am. J. Psychol.* 73, 2–21.

Lamy, D., Salti, M., and Bar-Haim, Y. (2009). Neural correlates of subjective awareness and unconscious processing: an ERP study. *J. Cogn. Neurosci.* 21, 1435–1446. doi: 10.1162/jocn.2009.21064

Lau, H. C., and Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 18763–18768. doi: 10.1073/pnas.0607716103

Lupyan, G., and Ward, E. J. (2013). Language can boost otherwise unseen objects into visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* 110, 14196–14201. doi: 10.1073/pnas.1303312110

Mack, A., and Rock, I. (1998). *Inattentional Blindness.* Cambridge, MA: MIT Press.

Marcel, A. J. (1983). Conscious and unconscious perception: experiments on visual masking and word recognition. *Cogn. Psychol.* 15, 197–237. doi: 10.1016/0010-0285(83)90009-9

Mudrik, L., Breska, A., Lamy, D., and Deouell, L. Y. (2011). Integration without awareness: expanding the limits of unconscious processing. *Psychol. Sci.* 22, 764–770. doi: 10.1177/0956797611408736

Peremen, Z., and Lamy, D. (2014). Do conscious perception and unconscious processing rely on independent mechanisms? A meta-contrast study. *Conscious. Cogn.* 24, 22–32. doi: 10.1016/j.concog.2013.12.006

Ramsøy, T. Z., and Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenol. Cogn. Sci.* 3, 1–23. doi: 10.1023/B:PHEN.0000041900.30172.e8

Raymond, J. E., Shapiro, K. L., and Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: an attentional blink? *J. Exp. Psychol. Hum. Percept. Perform.* 18, 849–860. doi: 10.1037/0096-1523.18.3.849

Rouder, J. N., Morey, R. D., and Pratte, M. S. (2013). Hierarchical Bayesian models. *Practice* 1, 1–50.

Sandberg, K., Timmermans, B., Overgaard, M., and Cleeremans, A. (2010). Measuring consciousness: is one measure better than the other? *Conscious. Cogn.* 19, 1069–1078. doi: 10.1016/j.concog.2009.12.013

Schmidt, T., and Vorberg, D. (2006). Criteria for unconscious cognition: three types of dissociation. *Percept. Psychophys.* 68, 489–504. doi: 10.3758/BF03193692

Schwiedrzik, C. M., Singer, W., and Melloni, L. (2009). Sensitivity and perceptual awareness increase with practice in metacontrast masking. *J. Vis.* 9, 1–18. doi: 10.1167/9.10.18

Shimaoka, D., and Kaneko, K. (2011). Dynamical systems modeling of continuous flash suppression. *Vision Res.* 51, 521–528. doi: 10.1016/j.visres.2011.01.009

Sklar, A. Y., Levy, N., Goldstein, A., Mandel, R., Maril, A., and Hassin, R. R. (2012). Reading and doing arithmetic nonconsciously. *Proc. Natl. Acad. Sci. U.S.A.* 109, 19614–19619. doi: 10.1073/pnas.1211645109

Stein, T., Hebart, M. N., and Sterzer, P. (2011). Breaking continuous flash suppression: a new measure of unconscious processing during interocular suppression? *Front. Hum. Neurosci.* 5:167. doi: 10.3389/fnhum.2011.00167

Sterzer, P., Stein, T., Ludwig, K., Rothkirch, M., and Hesselmann, G. (2014). Neural processing of visual information under interocular suppression: a critical review. *Front. Psychol.* 5:453. doi: 10.3389/fpsyg.2014.00453

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Van Opstal, F., Buc, C., Gevers, W., and Verguts, T. (2011). Setting the stage subliminally: unconscious context effects. *Conscious. Cogn.* 20, 1860–1864. doi: 10.1016/j.concog.2011.09.004

Vorberg, D., Mattler, U., Heinecke, A., Schmidt, T., and Schwarzbach, J. (2003). Different time courses for visual perception and action priming. *Proc. Natl. Acad. Sci. U.S.A.* 100, 6275–6280. doi: 10.1073/pnas.0931489100

Watanabe, M., Cheng, K., Murayama, Y., Ueno, K., Asamizuya, T., Tanaka, K., et al. (2011). Attention but not awareness modulates the BOLD signal in the human V1 during binocular suppression. *Science* 334, 829–831. doi: 10.1126/science.1203161

Wyart, V., and Tallon-Baudry, C. (2008). Neural dissociation between visual awareness and spatial attention. *J. Neurosci.* 28, 2667–2679. doi: 10.1523/JNEUROSCI.4748-07.2008

Yuval-Greenberg, S., and Heeger, D. J. (2013). Continuous flash suppression modulates cortical activity in early visual cortex. *J. Neurosci.* 33, 9635–9643. doi: 10.1523/JNEUROSCI.4612-12.2013

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 07 April 2014; accepted: 13 August 2014; published online: 11 September 2014.

Citation: Peremen Z and Lamy D (2014) Comparing unconscious processing during continuous flash suppression and meta-contrast masking just under the limen of consciousness. Front. Psychol. ***5****:969. doi: 10.3389/fpsyg.2014.00969*

This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 07 July 2014
doi: 10.3389/fpsyg.2014.00659

A direct comparison of unconscious face processing under masking and interocular suppression

Gregory Izatt[1†], **Julien Dubois**[1*†], **Nathan Faivre**[1,2†] **and Christof Koch**[1,3]

[1] Computation and Neural Systems, California Institute of Technology, Pasadena, CA, USA
[2] Laboratory of Cognitive Neuroscience, Brain Mind Institute, School of Life Sciences, École Polytechnique Fédérale de Lausanne, Lausanne, Switzerland
[3] Allen Institute for Brain Science, Seattle, WA, USA

Edited by:
Bernard J. Baars, The Neurosciences Institute, USA

Reviewed by:
Bernard J. Baars, The Neurosciences Institute, USA
Bernard Marius't Hart, Philipps-Universität Marburg, Germany

***Correspondence:**
Julien Dubois, Division of Biology 114-96 California Institute of Technology 1200 E California Blvd, Pasadena, CA 91125, USA
e-mail: jcrdubois@gmail.com

† These authors have contributed equally to this work.

Different combinations of forward and backward masking as well as interocular suppression have been used extensively to render stimuli invisible and to study those aspects of visual stimuli that are processed in the absence of conscious experience. Although the two techniques—masking vs. interocular suppression—obviously differ both in their applications and mechanisms, only little effort has been made to compare them systematically. Yet, such a comparison is crucial: existing discrepancies in the extent of unconscious processing inferred from these two techniques must be reconciled, as our understanding of unconscious vision should be independent of the technique used to prevent visibility. Here, we studied similarities and differences between faces rendered invisible by masking vs. interocular suppression using a priming paradigm. By carefully equating stimulus strength across the two techniques, we analyzed the effects of face primes with the same viewpoint (repetition priming, Experiment 1) and of face primes with a different viewpoint (identity priming, Experiment 2) on the reaction times for a fame categorization task. Overall, we found that the magnitude of both repetition and identity priming largely depended on stimulus visibility. Moreover, when the primes were subjectively invisible, both repetition and identity priming were found to be qualitatively stronger under masking than under interocular suppression. Taken together, these results help refine our understanding of which level of visual processing each technique disrupts, and illustrate the importance of systematic methodological comparisons in the field of unconscious vision.

Keywords: masking, backward masking, interocular suppression, continuous flash suppression, face processing, priming, awareness, consciousness

INTRODUCTION

In pursuing the neural correlates of consciousness, neuroscientists have developed a number of experimental techniques for suppressing conscious awareness of visual stimuli while still allowing some degree of unconscious processing (for review see Kim and Blake, 2005).

Arguably, two of the most used techniques employed to study unconscious vision are a combination of forward and backward masking and interocular suppression. In forward and backward masking, a high-contrast mask image is shown respectively before and after a briefly presented prime stimulus, rendering the prime undetectable (Breitmeyer and Ogmen, 2006). In interocular suppression (IS), an image in one eye is suppressed via the presentation of a high-contrast mask in the opposite eye (Tong et al., 2006; Lin and He, 2009); continuous flash suppression (CFS) extends this technique by updating the mask several times per second, which allows for long-lasting and powerful image suppression (Tsuchiya and Koch, 2005). It is not always clear why a researcher chooses one technique over the other to conduct a specific experiment, as justification is typically not required. One key determinant is the desired suppression time: whereas a combination of forward and backward masking (sometimes referred to as sandwich masking, but for the rest of the article for simplicity referred to as masking—abbreviated M) is mostly appropriate for brief presentation of unconscious stimuli, CFS allows longer unconscious stimulation (note that variations on masking may be used for longer suppression periods, see Macknik and Livingstone, 1998). Given that CFS relies on binocular interactions while masking does not, it is likely that these two techniques achieve subjective invisibility in fundamentally different ways.

A meta-analysis would unfortunately fall short of making strong claims about a possible difference in the depth of unconscious processing between the two techniques. Given the unavoidable idiosyncrasies of each published study, too many uncontrolled variables could account for any differences that would be found in a meta-analysis. Some authors have recently attempted to compare these two suppression techniques empirically. Kanai et al. (2010) measured the confidence in reporting the absence of a stimulus rendered invisible by several techniques including masking and IS; they found that both masking and IS disrupted stimulus visibility by reducing the strength of sensory (input) signals, but other techniques such as the attentional blink disrupted attentional access to the sensory signals instead. Focusing on the processing of emotional faces, Stein et al. (2013) showed that visibility of emotional faces was mostly driven by high spatial frequencies both under masking and IS. Hence within the scope of these two studies, no difference was found between how masking and IS prevent visibility. Yet, the two techniques obviously find their origins in distinct mechanisms: for one thing, masking is monocular while IS is binocular (see Breitmeyer and Ogmen, 2006 for review). One may thus expect to find differences in the depth of processing allowed by each of the two techniques. In an influential study, Almeida and colleagues found that masking, but not IS, allowed for unconscious processing of non-manipulable objects (i.e., animal pictures) along the ventral visual pathways (Almeida et al., 2008). Looking at the processing of emotional faces, Faivre et al. (2012) failed to find a difference between masking and IS: in their hands, only low-level facial features were processed when emotional faces were rendered invisible by masking or IS (they also found that more complex features such as those encoding happy facial expressions were processed in similar conditions of invisibility in a crowding paradigm). Almeida et al. (2013) challenged this result: they reported that features conveying the expression of happiness and anger were indeed processed when rendered invisible by masking, but only the features conveying anger were processed under IS. The authors suggested a dissociation between a subcortical route involved in the processing of anger (available under both masking and IS), and a cortical route for the processing of happiness (available under masking only). Though these published studies report conflicting results, they illustrate an increasing concern regarding the possibility that unconscious processes may differ under different suppression techniques.

Not only is it necessary to compare two techniques within the same study (as in the few studies that we briefly reviewed above), it is also crucial to carefully equate as many parameters as possible between the techniques under scrutiny. Here, we sought to examine the differences in unconscious processing under masking and IS while matching stimulation conditions to the best of our ability. We chose a fame categorization task with a priming paradigm, building on previous results in the literature (Henson et al., 2008; Kouider et al., 2009). Priming effects have been used extensively as a measure of unconscious processing: they quantify whether the presence of an invisible stimulus facilitates the processing of a target stimulus sharing some similarities with that invisible prime (Kiesel et al., 2007). By varying the type of information shared between the prime and target, one can infer the level of processing undergone by the prime (e.g., from low-level featural information like orientation or color, to high-level information like semantic or emotional content). In this study, we chose to focus on the processing of face identity. There is compelling evidence for face identity processing under masking (see Kouider and Dehaene, 2007 for review); however, several studies suggest that the processing of face identity is disrupted under IS (see Faivre et al., 2014, in this volume for a review). Notably, identity after-effects (i.e., a bias for the perception of a specific face after the observer adapts to a face that has opposite global features) vanished when the face adaptor was rendered invisible by interocular suppression (Moradi et al., 2005). We looked into this apparent difference in unconscious processing depth between the two techniques using both repetition and identity priming effects for both famous and unfamiliar faces, with the hypothesis that we would replicate previous repetition and identity priming effects under masking, but find only repetition priming under IS. We randomly used masking or IS on each trial to render the primes invisible; the stimuli were carefully designed in such a way that participants did not notice this manipulation. We investigated two levels of face identity representation: viewpoint-dependent (i.e., repetition priming, Experiment 1) and viewpoint-independent (i.e., identity priming, Experiment 2). By varying the mask contrast used in masking and IS, we looked at repetition and identity priming effects as a function of stimulus visibility under each technique. While we did not find definite evidence supporting our specific prediction, we discovered variations in effect sizes between masking and IS indicating subtle differences between the two techniques.

MATERIALS AND METHODS

PARTICIPANTS

Forty four subjects participated in the study—18 (7 male, 11 female) for an experiment utilizing same-view priming (Experiment 1), and 26 (11 male, 15 female) for an experiment utilizing different-view priming (Experiment 2). All subjects were between 20 and 35 of age, reported normal or corrected-to-normal vision, and gave written statements of informed consent to participate in the study. All experiments conformed to Institutional Guidelines and to the Declaration of Helsinki.

APPARATUS

Stimuli were displayed on a Mitsubishi Diamond pro 2070 1024 × 768 px CRT monitor with a 100 Hz refresh rate. Subjects viewed the stimuli from a distance of 40 cm, through a set of mirrors, such that the left eye saw the left half of the screen, and the right eye saw the right half of the screen. The experiment was written and executed using Matlab and Psychophysics toolbox version 3.1 (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). Statistical analysis was performed using Matlab and R (R Foundation for Statistical Computing Vienna, Austria).

STIMULI

The set of famous faces comprised 31 females and 30 males, all famous actors or politicians within the United States (for names, see Supplementary Table 1). The set of unfamiliar faces comprised 10 females and 10 males; they were, in fact, pictures of Israeli celebrities that were chosen to ensure rough equivalence in attractiveness and image quality with the famous faces. All face images used in the experiment were processed to remove most low level differences: they were converted to gray scale then normalized using a combination of in-house Matlab code and functions from the SHINE toolbox (Willenbockel et al., 2010 and **Figure 1**). Raw face images were 400 × 400 px in size. Our normalization procedure included the following steps: image transformation to match face sizes and positions based on manually annotated eye and mouth points (using Procrustes analysis, i.e., translation, rotation and global scaling); application of a Gaussian aperture and blur to remove image background and borders; and image histogram equalization over the entire set of face images. Histogram equalization was performed only on manually annotated face regions in each image, such that background color remained uniform across all stimuli. Targets and masks were finally scaled to occupy a visual angle of 13.5°, and primes 11.1°. The masks consisted of randomly generated white, black, and gray filled ovals superimposed onto each other (the dimensions of the oval shapes ranged between 4 and 22% of the size of the masks; 1000 oval shapes were randomly generated and pasted sequentially at random locations within each mask); we generated a pool of 1000 such masks, which we sampled from randomly, without replacement, in each trial.

PROCEDURE

Upon arrival, participants were asked to look over the set of famous male and female faces, from which they picked a subset of 10 of each gender that they were most familiar with. In Experiment 1, subjects were exposed to frontal views of each face; in Experiment 2, subjects were exposed to both frontal and profile views of each face, and were told to only choose faces which they could recognize from both points of view. Subjects who did not feel sufficiently familiar with the faces to accomplish the task were not tested further. Only one subject was rejected at this stage. No subject reported familiarity with any the 20 unfamiliar faces.

Each trial began with a fixation cross that stayed on the screen until a button press (**Figure 2**). The subjects' main task was to categorize a target image as famous or unfamiliar as fast as possible using the arrow keys (using the right and left arrow keys on the keyboard respectively, with the ring and index fingers of the right hand). The masking technique in each trial was randomly chosen as either masking or interocular suppression (IS). In masking trials, eight different masks (to match the sequence of mask in interocular suppression) were presented for 100 ms each, followed by a 50 ms prime, a 50 ms mask, and finally a 700 ms target image; all masks, the prime, and the target image were presented to the subject's non-dominant eye, while isoluminant gray was presented to the dominant eye. In IS trials, all masks were presented to the dominant eye, while the prime and the target image were presented to the non-dominant eye. The sequence and timing of masks, prime, and target image was the same as in masking, with the exception that the first mask in the eight-mask sequence was removed to counterbalance the addition of a mask shown simultaneously with the prime (necessary to induce interocular

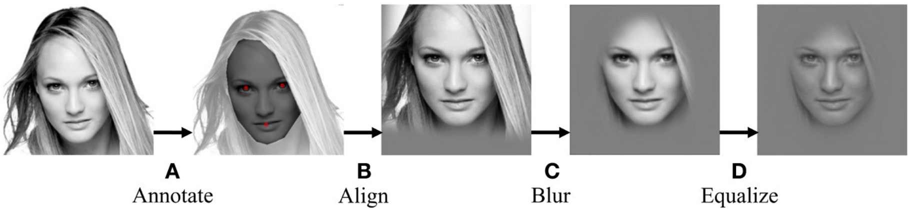


FIGURE 1 | The image normalization procedure, as executed on an unfamiliar female face. (A) The experimentalist supplies annotation of mouth and eye locations. **(B)** These are used to center and scale the face to a standard shared across images; resulting visible image borders are blurred to gray. **(C)** A tight aperture is applied to the image. **(D)** The SHINE toolbox for MATLAB (Willenbockel et al., 2010) is used to normalize image histograms over the entire dataset.

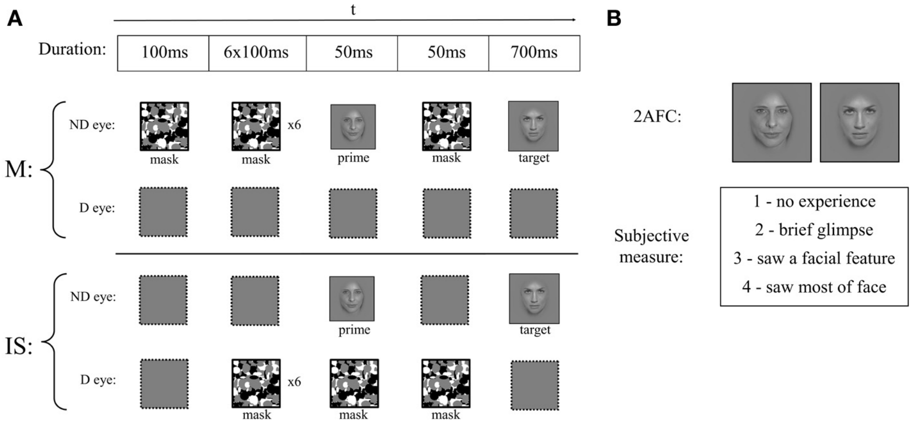


FIGURE 2 | A schematic depiction of a single trial that required subjects to make 3 responses. (A) Each trial was displayed with either masking (M) or interocular suppression (IS) applied to the prime. The sequence of images presented to the subjects' non-dominant (ND) and dominant (D) eye is shown. In masking, which is a combination of forward and backward masking, nothing is presented to the D eye, while under interocular suppression, masks are presented to the D eye and primes and targets are presented to the ND eye. Subjects had to categorize the target as famous or unfamiliar as quickly as possible using two arrow keys. **(B)** After categorization, they were asked to indicate which face was presented as a prime among two alternatives (2-AFC objective visibility measure) and, immediately afterwards, to indicate the subjective experience they had about the prime on a 4-point Perceptual Awareness Scale (subjective visibility measure).

suppression). There was no enforced time-out; however if subjects took longer than 1.2 s on the speeded target categorization task, they were presented with a penalizing "Too Slow!" message for 2 s. Two questions aimed at assessing trial-by-trial visibility followed the target categorization task. First, a two-alternative forced choice task (2-AFC) in which two faces were shown side-by-side and subjects had to pick which of the two was shown as the prime face. The choices were always faces from the same viewpoint as the prime (see Experimental Design below). The target image (or, in Experiment 2, the same identity as the target image, seen from a different viewpoint) was always one of the choices, with the other image being chosen to ensure that the prime was always available as a choice (i.e., if prime and target were the same, the second image would be a random other image with the same fame; otherwise, the other image would be the prime). This 2-AFC served as an objective measure of visibility. Second, subjects rated their subjective experience of the prime using the following options "1—no experience"; "2—brief glimpse"; "3—saw a facial feature"; and "4—saw most of face." Importantly, they were instructed that "2—brief glimpse" meant they detected some shapeless luminance blob in which they did not detect any facial features (as opposed to "3—saw a facial feature"). This served as a subjective measure of visibility (Ramsøy and Overgaard, 2004). Note that subjects always performed a practice version of the task for several minutes to ensure that they understood instructions properly.

EXPERIMENTAL DESIGN

The relationship between the target and the prime was varied in a controlled manner across trials. Primes and targets were always gender and fame matched, to minimize response congruity effects (Damien, 2001; Kouider et al., 2009). In trials of the same-view priming experiment (Experiment 1), both the prime and the target were drawn from a set of front-view-only faces. Priming relationship could thus either be "same view, different identity (same fame)" (e.g., a front-view face X as a prime, followed by another front-view face Y as a target, both being either famous or unfamiliar) or "same view, same identity" (e.g., a front-view face X as a prime, followed by the same front-view face X as a target). In trials of the different-view priming experiment (Experiment 2), the targets were drawn from the same set of front-view-only faces as in Experiment 1, while the primes were drawn from a set of corresponding quarter-profile-view faces. Priming relationships could thus be "different view, different identity (same fame)" (e.g., quarter-profile-view face X as a prime, followed by the front-view face Y as a target, both being either famous or unfamiliar) or "different view, same identity" (e.g., quarter-profile-view face X as a prime, followed by the front-view face X as a target). To minimize priming across trials (for example, if target face X is presented on trials *n-1* and *n*, the response on trial *n* is likely to be sped up), we ensured that a given famous or unfamiliar face was never seen in consecutive trials as either the prime, the target, or the alternate choice in the 2-AFC question. Note that primes were scaled to be 80% the size of targets in order to minimize pixel overlap in Experiment 1, as has been done in previous studies (Kouider et al., 2009). For consistency, primes were also scaled to 80% in Experiment 2 (even though pixel overlap was not a concern). We had three levels of masks contrast to vary masking strength across trials: 2, 40, and 60% (Michelson contrast). Pilot experiments suggested that these values were associated respectively to conditions of full visibility, partial visibility, and null visibility of the primes. Both experiments were broken up in blocks of 144 trials, each containing six repetitions of each condition; subjects completed as many blocks (up to five) as they could within 90 min.

ANALYSIS

Five subjects (three in Experiment 1, two in Experiment 2) with below 70% accuracy on the target categorization task were excluded from analysis (their low accuracy indicates that they were not familiar enough with the famous faces; also, since all trials for which target categorization was incorrect are removed from the analysis, the number of trials for these subjects becomes too low for accurate estimates of priming effects). Across the remaining subjects, the first 10 trials were discarded to allow subjects to reach a stable strategy, as were trials in which they categorized the target incorrectly (as mentioned above), too quickly compared to a hard threshold (reaction times less than 200 ms were excluded), or too quickly or slowly as measured by a deviation of more than two standard deviations from each subject's mean reaction time. After these restrictions, if for any subject the number of trials for a given mask contrast, target fame, masking technique and prime-target relationship was less than or equal to five, all trials for that subject at that mask contrast were discarded (all trials at that mask contrast were discarded, instead of just trials within the specific combination of mask contrast, target fame, masking technique and prime-target relationship, to maintain a balanced design for ANOVAs within each mask contrast). In order to satisfy assumptions of data normality, we performed statistical tests on the inverse of reaction times (Whelan, 2008).

Transformed reaction times were analyzed with 3 × 2 × 2 × 2 repeated measures ANOVA, with mask contrast, masking technique, target fame, and prime-target relationship as within subject factors, and subjects as a random variable. Priming effects were calculated by subtracting mean reaction times in the unrelated (different identity) vs. related (same identity) conditions. Therefore, positive priming values reflect a decrease of reaction times in related vs. unrelated trials. Where significant interactions arose, planned *t*-tests were performed. Similar ANOVAs run on accuracies in the target categorization task did not yield any significant effects. Finally, similar ANOVAs were run on accuracies in the objective visibility task in order to estimate the visibility of the primes. No correction for multiple comparisons was performed.

RESULTS

The number of trials for each subject after the eliminations described in Materials and Methods are listed in Supplementary Tables 2, 3. Qualitative Q-Q plots demonstrating the utility of the inverse transform in upholding the assumption of normality are shown in Supplementary Figures 1–4. No subject independently reported being able to differentiate the different masking techniques.

EXPERIMENT 1

Priming effects are displayed in **Table 1**. We started by running a 3 × 2 × 2 × 2 repeated measures ANOVA across all trials without selection by subjective visibility rating (**Figure 3**; see Materials and Methods). It showed a main effect of relation [$F_{(1,\ 14)} = 33.09$, $p < 0.001$], indicating that participants categorized the fame of a target face faster when it was preceded by an identical then by a different prime face (i.e., repetition priming effect, mean reaction times difference = 18 ms, $SD = 16$ ms). The same analysis also showed a main effect of target fame [$F_{(1,\ 14)} = 23.96$, $p < 0.001$], and mask contrast [$F_{(2,\ 28)} = 7.28$, $p = 0.003$], indicating respectively that participants responded faster to famous than to unfamiliar faces (mean reaction times difference = 44 ms, $SD = 36$ ms), and to low than to high mask contrasts (weak contrast: 641 ms, $SD = 64$ ms; medium contrast: 651 ms, $SD = 56$ ms; high contrast: 656 ms, $SD = 53$ ms).

The ANOVA also showed an interaction between relation and target fame [$F_{(1,\ 14)} = 11.28$, $p = 0.005$], between relation and mask contrast [$F_{(2,\ 28)} = 42.82$, $p < 0.001$], and between target fame and mask contrast [$F_{(2,\ 28)} = 4.72$, $p = 0.017$]. These interactions respectively revealed that priming effects were larger for famous than for unfamiliar faces (mean priming difference = 9 ms, $SD = 20$ ms), decreased as mask contrast increased (weak contrast: 44 ms, $SD = 29$ ms; medium contrast: 13 ms, $SD = 15$ ms; high contrast: −1 ms, $SD = 16$ ms), and that mask contrast affected reaction times more for famous faces (weak contrast: 613 ms, $SD = 52$ ms; medium contrast: 631 ms, $SD = 50$ ms; high contrast: 637 ms, $SD = 53$ ms) than for unfamiliar faces (weak contrast: 668 ms, $SD = 80$ ms; medium contrast: 672 ms, $SD = 69$ ms; high contrast: 674 ms, $SD = 58$ ms) (though this last interaction is unrelated to the priming effects, we report it here for completeness).

Finally, we found a triple interaction between relation, mask contrast, and target fame [$F_{(2,\ 28)} = 8.92$, $p = 0.001$], suggesting that the magnitude of priming effects decreased more as mask contrast increased for famous than for unfamiliar faces. No other effect reached significance (p-values > 0.28).

Importantly, no effect of technique (i.e., masking vs. interocular suppression) reached significance ($p > 0.28$). That is, the

Table 1 | Reaction time priming effect sizes for Experiment 1.

Method	Fame	Contrast	All Subj. Vis.		Subj. Vis. 1-2	
			Effect (ms)	*SD* (ms)	Effect (ms)	*SD* (ms)
M	Famous	1	59	31	–	–
IS	Famous	1	57	39	–	–
M	Unfamiliar	1	27	36	–	–
IS	Unfamiliar	1	32	43	–	–
M	Famous	2	17	25	14	32
IS	Famous	2	4	33	15	41
M	Unfamiliar	2	20	20	18	24
IS	Unfamiliar	2	9	41	6	42
M	Famous	3	0	33	−7	38
IS	Famous	3	2	27	6	24
M	Unfamiliar	3	4	29	5	35
IS	Unfamiliar	3	−10	23	−9	25

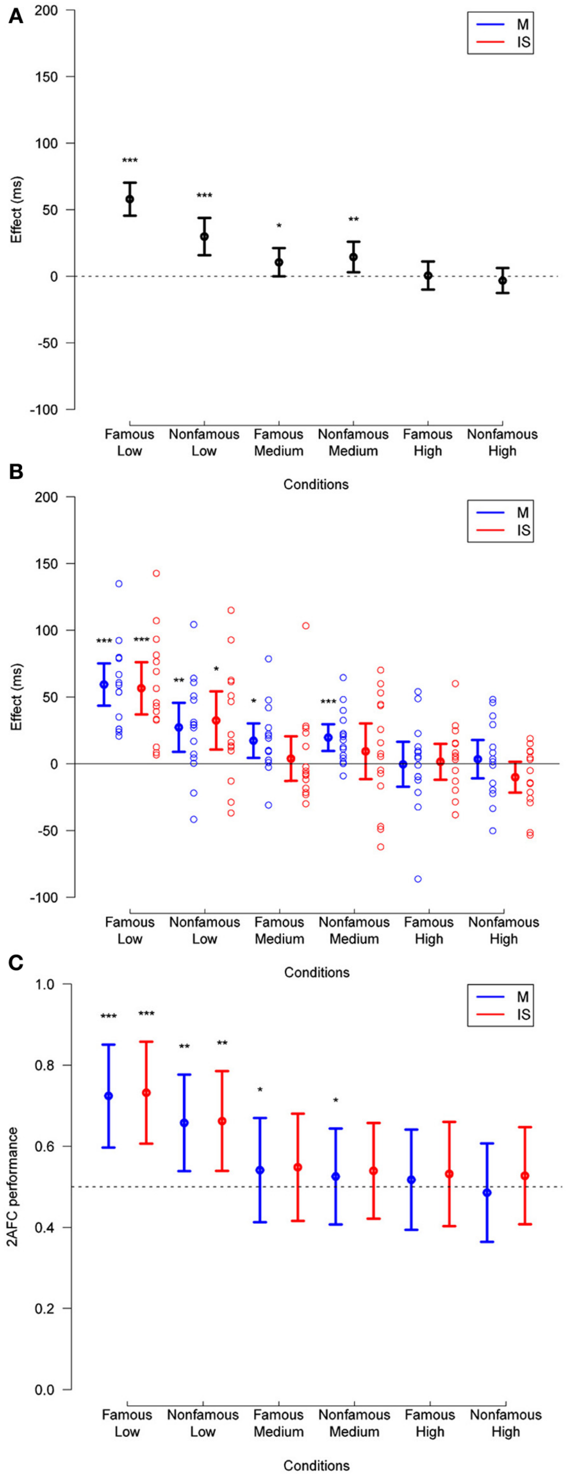


FIGURE 3 | (A) Priming effect observed in Experiment 1, across fame of target and prime (famous or unfamiliar), and mask contrast levels (low, medium, or high), for trials with any subjective visibility rating. **(B)** Same data broken down by masking method. The data for individual subjects is shown (empty circles). **(C)** Corresponding 2-AFC performance is collapsed across relation. In all plots, deviation of effects from a null hypothesis are measured in paired *t*-tests, and are not corrected. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

magnitude of differences in reaction times was not affected by which one of the two techniques rendered the prime invisible.

Regarding stimulus visibility, a 3 × 2 × 2 × 2 repeated measures ANOVA across the same trials showed main effects of target fame [$F_{(1,\ 14)} = 10.84$, $p = 0.005$] and mask contrast [$F_{(1,\ 14)} = 13.16$, $p < 0.001$]. That is, accuracy on the objective visibility task was higher for famous (mean = 0.60, $SD = 0.09$) than for unfamiliar faces (mean = 0.57, $SD = 0.07$) and it decreased as mask contrast increased (weak contrast: 0.69, $SD = 0.19$; medium contrast: 0.54, $SD = 0.058$; high contrast: 0.52, $SD = 0.048$). The ANOVA also revealed an interaction between target fame and mask contrast [$F_{(2,\ 28)} = 4.27$, $p = 0.024$]; that is, the strength of masking had a higher impact on famous than on unfamiliar faces (mean of the accuracy difference, i.e., famous accuracy minus unfamiliar accuracy; at weak mask contrast: 0.068, $SD = 0.075$; medium mask contrast: 0.012, $SD = 0.050$; high mask contrast: 0.018, $SD = 0.055$). No other effect reached significance (p-values > 0.21).

Taken together, as the ANOVA showed an impact of mask contrast on priming independently of the technique (i.e., no effect of technique reached significance), the results suggest masking and IS have a similar detrimental effect on the magnitude of repetition priming.

In order to test for the existence of unconscious repetition priming under masking and IS, we repeated the same analysis but only on those trials in which participants either reported "no experience," or "a brief glimpse" of the prime (**Figure 4**; see Materials and Methods). With additional elimination due to a decreased number of trials in each condition (see Materials and Methods), this reduced total trials by 26.1% relative to the previous analysis. Subjective visibility ratings, averaged across subjects, mask contrast, target fame, and masking technique, are presented in Supplementary Figure 5. This analysis included only medium and high mask contrast, as only 6 subjects fulfilled the selection criteria (see Materials and Methods) in the weak mask contrast condition (this is, of course, expected: the weak mask contrast lead to mostly visible trials).

This analysis showed a main effect of target fame [$F_{(1,\ 12)} = 13.90$, $p = 0.003$], and mask contrast [$F_{(1,\ 12)} = 5.83$, $p = 0.03$], revealing that participants responded faster to famous faces than to unfamiliar faces (mean reaction times difference = 36 ms, $SD = 36$ ms), and to medium than to high mask contrasts (mean reaction times difference = 5 ms, $SD = 11$ ms). Here, the main effect of relation was not significant [$F_{(1,\ 12)} = 4.42$, $p = 0.055$; mean reaction times difference = 6 ms, $SD = 14$ ms]; that is, we could not reject the hypothesis of no repetition priming, over all conditions. The ANOVA did show an interaction between relation and mask contrast [$F_{(1,\ 12)} = 7.1$, $p = 0.02$], revealing that priming effects decreased as mask contrast increased (at medium mask contrast: 13 ms, $SD = 15$ ms, $t_{(12)} = 3.11$, $p = 0.009$; at high mask contrast: −1 ms, $SD = 19$ ms, $t_{(12)} = -0.23$, $p = 0.82$). Again, no effect of masking technique reached significance (p-values > 0.19).

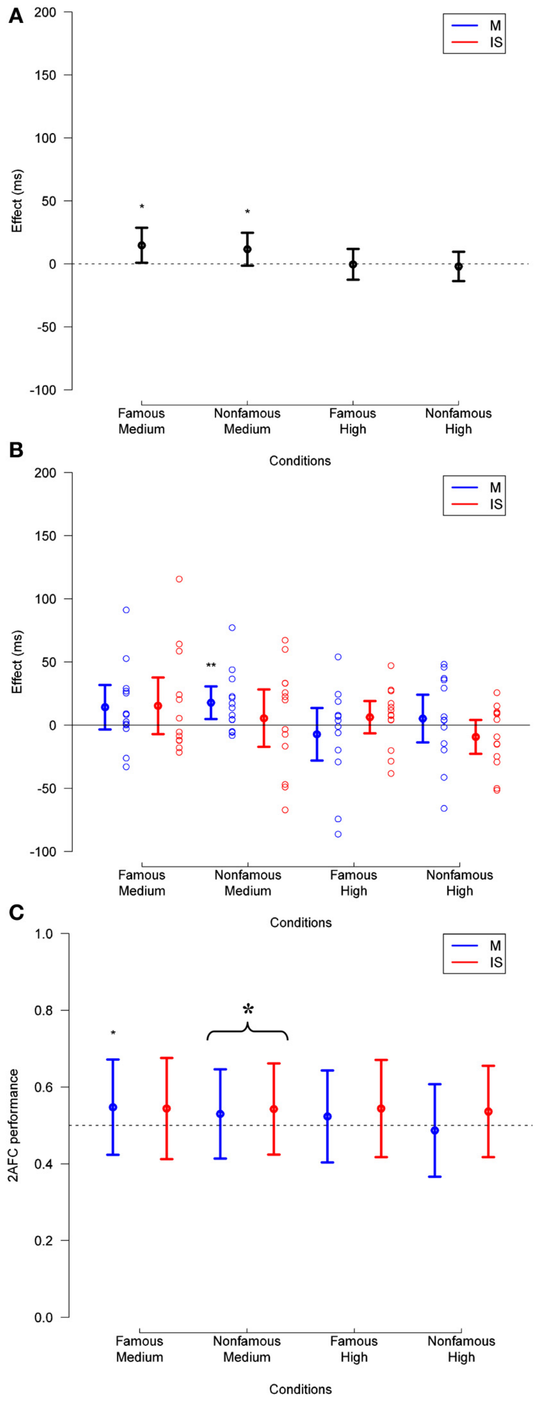


FIGURE 4 | As in Figure 3 except for only those trials in which the visibility was 1 or 2. Deviation of 2-AFC performance from chance when collapsed across method (as reported in Results) is also displayed in **(C)**. See legend to **Figure 3** for other details.

Regarding stimulus visibility, a 2 × 2 × 2 × 2 repeated measures ANOVA across the same trials showed an interaction between target fame and mask contrast [$F_{(1,\ 12)} = 7.88$, $p = 0.02$], revealing that the strength of masking had a higher impact on famous than on unfamiliar faces (mean of the accuracy difference at medium mask contrast: 0.0095, $SD = 0.058$; high mask contrast: 0.02, $SD = 0.060$). No other effect reached significance (p-values > 0.06).

In addition, *post-hoc* one-sample t-tests revealed that 2-AFC performance across mask strength differed from chance for unfamiliar faces [mean = 0.54, $t_{(12)} = 2.54$, $p = 0.03$], but did not differ significantly for famous faces [mean = 0.55, $t_{(12)} = 1.93$, $p = 0.08$]. For the high mask contrast, 2-AFC performance was indistinguishable from chance for both famous [mean = 0.53, $t_{(12)} = 2.11$, $p = 0.06$] and unfamiliar faces [mean = 0.51, $t_{(12)} = 0.75$, $p = 0.50$].

At medium mask contrast, repetition priming was significant for masking [16 ms, $t_{(12)} = 3.54$, $p = 0.004$], but not under IS [10 ms, $t_{(12)} = 1.71$, $p = 0.11$]. Separating by the fame of the target, repetition priming remains significant for masking for unfamiliar faces [18 ms, $t_{(12)} = 3.14$, $p = 0.009$], but loses significance for famous faces [14 ms, $t_{(12)} = 1.91$, $p = 0.081$], and remains non-significant for IS for both famous [15 ms, $t_{(12)} = 1.39$, $p = 0.19$] and unfamiliar [6 ms, $t_{(12)} = 0.90$, $p = 0.39$] faces. No repetition priming was found at high mask contrast (p-values > 0.32).

These results suggest that, if awareness is defined according to subjective visibility (subjects report seeing nothing, or a brief glimpse with no content), unconscious repetition priming occurs under masking at medium, but not high mask contrast. Priming appeared slightly more robust under masking than under IS, but no significant difference of priming depending on the technique reached significance in the ANOVA. Note that if we define awareness with the objective 2-AFC performance measure, no claim of unconscious priming can be made because subjects were on average slightly above chance (**Figures 3C**, **4C**). We come back to these issues in the discussion.

EXPERIMENT 2

Priming effects are displayed in **Table 2**. We tested for viewpoint-independent priming in this experiment by running a 3 × 2 × 2 × 2 repeated measures ANOVA across all trials without selection by subjective visibility rating (see Materials and Methods and **Figure 5**). It showed a main effect of relation [$F_{(1,\ 22)} = 9.48$, $p = 0.006$], target fame [$F_{(1,\ 22)} = 33.60$, $p < 0.001$], and mask contrast [$F_{(2,\ 45)} = 7.50$, $p = 0.002$]. As in Experiment 1, these

Table 2 | Reaction time priming effect sizes for Experiment 2.

Method	Fame	Contrast	All Subj. Vis.		Subj. Vis. 1-2	
			Effect (ms)	SD (ms)	Effect (ms)	SD (ms)
M	Famous	1	21	30	15	33
IS	Famous	1	9	37	15	44
M	Unfamiliar	1	2	45	1	57
IS	Unfamiliar	1	9	29	9	34
M	Famous	2	18	24	14	24
IS	Famous	2	13	30	13	29
M	Unfamiliar	2	6	28	4	32
IS	Unfamiliar	2	−5	25	−7	24
M	Famous	3	−3	24	−5	28
IS	Famous	3	−4	23	−2	28
M	Unfamiliar	3	−8	28	−11	31
IS	Unfamiliar	3	6	30	5	33

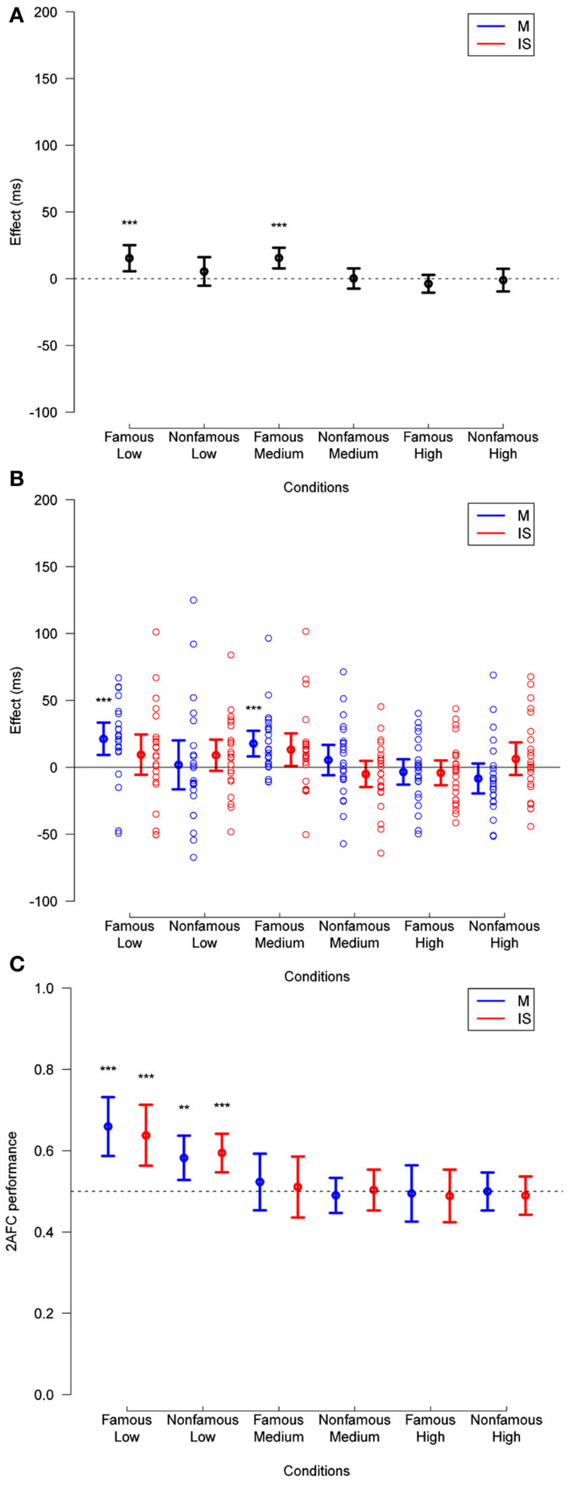


FIGURE 5 | (A) Priming effect observed in Experiment 2, across fame of target and prime (famous or unfamiliar), and mask contrast levels (low, medium, or high), for trials with any subjective visibility rating. **(B)** Same data broken down by masking method. The data for individual subjects is shown (empty circles). **(C)** Corresponding 2-AFC performance is presented collapsed across relation. In all plots, deviation of effects from a null hypothesis are measured in paired t-tests, and are not corrected. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

effects were respectively due to participants responding faster in related than in unrelated trials (i.e., priming effect: mean reaction times difference = 6 ms, $SD = 9$ ms), famous vs. unfamiliar faces (mean reaction times difference = 44 ms, $SD = 37$ ms), and low vs. high mask contrasts (weak contrast: 661 ms, $SD = 67$ ms; medium contrast: 669 ms, $SD = 64$ ms; high contrast: 675 ms, $SD = 66$ ms).

The ANOVA also showed an interaction between relation and target fame [$F_{(1,\ 22)} = 8.90$, $p = 0.007$], between relation and mask contrast [$F_{(2,\ 45)} = 8.68$, $p < 0.001$]. These interactions respectively revealed that priming effects were larger for famous than for unfamiliar faces (mean reaction times difference = 8 ms, $SD = 18$ ms), and that priming effects decreased as mask contrast increased (weak contrast: 10 ms, $SD = 17$ ms; medium contrast: 8 ms, $SD = 14$ ms; high contrast: −2 ms, $SD = 14$ ms).

Finally, we found a triple interaction between relation, mask contrast, and target fame [$F_{(2,\ 45)} = 3.47$, $p = 0.040$], suggesting that the magnitude of priming effects decreased more as mask contrast increased for famous than for unfamiliar faces (**Figure 6**), and a triple interaction between masking technique, mask contrast, and target fame [$F_{(2,\ 45)} = 4.54$, $p = 0.016$], revealing that the difference in reaction time between masking and IS depended more strongly on mask contrast for famous faces (weak contrast: 8 ms, $SD = 18$ ms; medium contrast: −3 ms, $SD = 28$ ms; high contrast: 12 ms, $SD = 25$ ms) than for unfamiliar faces (weak contrast: 1 ms, $SD = 21$ ms; medium contrast: 2 ms, $SD = 29$ ms; high contrast: −2 ms, $SD = 26$ ms) (this effect is somewhat irrelevant, but reported for completeness). No other effect reached significance (p-values > 0.10).

Regarding stimulus visibility, a 3 × 2 × 2 × 2 repeated measures ANOVA across the same trials showed main effects of target fame [$F_{(1,\ 22)} = 7.28$, $p = 0.013$] and mask contrast [$F_{(2,\ 45)} = 25.66$, $p < 0.001$], revealing that accuracy on the objective visibility task was higher for famous (mean = 0.55, $SD = 0.059$) than for unfamiliar faces (mean = 0.53, $SD = 0.040$), and that it decreased as mask contrast increased (weak contrast: 0.62, $SD = 0.10$; medium contrast: 0.51, $SD = 0.050$; high contrast: 0.49, $SD = 0.037$). The ANOVA also revealed an interaction between target fame and mask contrast [$F_{(2,\ 45)} = 4.27$, $p = 0.010$], revealing that the strength of masking had a higher impact on performance for famous than for unfamiliar faces (mean of the accuracy difference at weak mask contrast: 0.06, $SD = 0.087$; medium mask contrast: 0.02, $SD = 0.056$; high mask contrast: −0.0030, $SD = 0.068$). No other effect reached significance (p-values > 0.09).

In order to test for the existence of unconscious identity priming under masking and IS, we ran the same 3 × 2 × 2 × 2 repeated measures ANOVA on trials in which participants reported having "no experience," or just seeing "a brief glimpse" of the prime (see Materials and Methods). This eliminated an additional 12.8% of the total trials relative to the previous analysis. Subjective visibility ratings, averaged across subject, mask contrast, target fame, and masking technique, are presented in Supplementary Figure 6. As opposed to Experiment 1, we obtained enough trials at weak mask contrast to include this condition in the following analysis (**Figure 6**).

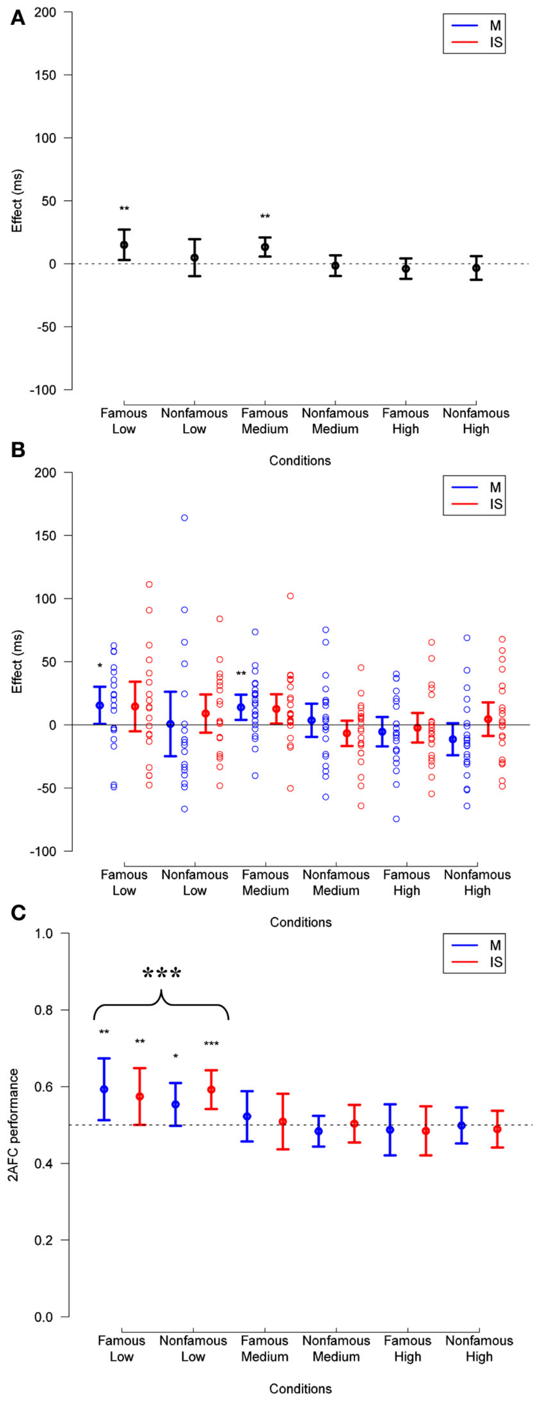


FIGURE 6 | As in Figure 5 except for only those trials in which the visibility was rated 1 or 2. Deviation of 2-AFC performance from chance when collapsed across fame and method (as reported in Results) is also displayed in **(C)**. See legend to **Figure 5** for other details.

This analysis showed a main effect of mask contrast [$F_{(2,\ 40)} = 7.09$, $p = 0.002$], and target fame [$F_{(1,\ 21)} = 32.60$, $p < 0.001$], revealing that reaction times were longer as mask contrast increased (weak: 663 ms, $SD = 64$ ms; medium: 672 ms, $SD = 61$ ms; high: 680 ms, $SD = 63$ ms), and shorter for famous than for unfamiliar faces (mean reaction times difference = 42 ms, $SD = 38$ ms). The main effect of relation was not significant [$F_{(1,\ 21)} = 3.59, p = 0.072$], suggesting that participants' response time in related vs. unrelated trials (i.e., priming effect, considered across all other conditions) was similar (mean reaction times difference = 3 ms, $SD = 10$ ms).

The ANOVA also showed an interaction between relation and mask contrast [$F_{(2,\ 40)} = 5.98$, $p = 0.005$], revealing that priming effects decreased as mask contrast increased. *Post-hoc* t-tests revealed that identity priming was significant at weak mask contrast [10 ms, $SD = 19$ ms, $t_{(18)} = 2.77$, $p = 0.012$] but not at medium mask contrast [6 ms, $SD = 13$ ms; $t_{(22)} = 1.85$; $p = 0.078$], nor at high mask contrast: [−4 ms, $SD = 15$ ms, $t_{(22)} = -1.22$, $p = 0.24$]. No other effects reached significance (p-values > 0.075).

Regarding stimulus visibility, a 3 × 2 × 2 × 2 repeated measures ANOVA across the same trials showed a main effect of mask contrast [$F_{(2,\ 40)} = 12.84$, $p < 0.001$]. Exploratory one-sample t-tests revealed that 2-AFC performance across a given mask strength differed from chance at the lowest mask contrast [mean = 0.58, $t_{(18)} = 4.36$, $p < 0.001$]. For the middle and high mask contrasts, 2-AFC performance was indistinguishable from chance [mean = 0.50, $t_{(22)} = 0.45$, $p = 0.65$ and mean = 0.49, $t_{(22)} = -1.20$, $p = 0.24$ respectively]. No other effect in the ANOVA reached significance (p-values > 0.13).

Post-hoc t-tests revealed that at medium mask contrast (i.e., the one at which unconscious processing is most likely to occur according to the visibility analysis described above), identity priming was significant for famous faces for masking [14 ms, $SD = 5$ ms, $t_{(22)} = 3.22$, $p = 0.004$], but not for IS [13 ms, $SD = 6$ ms, $t_{(22)} = 1.71$, $p = 0.10$]. Identity priming was not significant for unfamiliar faces under either masking [4 ms, $SD = 7$ ms, $t_{(22)} = 0.18$, $p = 0.86$] or IS [−7 ms, $SD = 5$ ms, $t_{(22)} = -1.00$, $p = 0.33$]. As opposed to what we found in Experiment 1, this suggests that unconscious identity priming is more robust for famous than for unfamiliar faces, and similarly to Experiment 1, for masking than for IS. However, a paired t-test between masking techniques at the medium mask contrast did not reveal a difference in famous identity priming [$t_{(22)} = 0.53$, $p = 0.60$], unfamiliar identity priming [$t_{(22)} = 0.46$, $p = 0.65$], or a collapsed condition [$t_{(22)} = 0.61$, $p = 0.55$].

DISCUSSION

In this work, we assessed the influence of a combination of forward and backward masking (referred to simply as "masking") and interocular suppression (IS) on face processing. We took great care in carefully equalizing as many parameters as possible between the two techniques. This is the novel aspect of our study in contrast to previous studies that compared suppression techniques (Almeida et al., 2008, 2010, 2013; Kanai et al., 2010; Faivre et al., 2012; Stein et al., 2013); critically, the duration and energy of the masked stimulus was the same across the two suppression methods.

We respectively used repetition priming (Experiment 1) and identity priming (Experiment 2) as an index of low-level and high-level face processing. By manipulating mask contrast while keeping the prime contrast constant, we found that both masking and IS affected repetition and identity priming effects, as revealed by a decrease in priming magnitude when mask contrast increased. In both experiments, priming was virtually abolished at the highest mask contrast, which corresponded to chance-level performance in the objective visibility task. These results suggest that masking and IS already interfere before (or at the level of) low-level face processing as indexed by repetition priming. This is in line with previous results showing that the magnitude of tilt and motion after-effects (considered low-level effects) decreased when the strength of suppression by binocular rivalry and crowding increased (Blake et al., 2006).

Looking beyond this obvious general trend in our results, priming effects and prime visibility could be dissociated for masking at medium mask contrast. In Experiment 1, famous and unfamiliar faces induced repetition priming when considering only trials in which subjects reported not seeing the primes (note however that performance in the objective visibility task differed slightly from chance level). In Experiment 2, selecting the low visibility trials, only famous faces induced identity priming (and in that experiment, the objective measure of visibility was at chance). The fact that unfamiliar faces elicited repetition but not identity priming is consistent with the idea that unconscious repetition priming stems from low-level processes (possibly at the level of primary visual cortex, see Faivre and Koch, 2014), while unconscious identity priming stems from preexisting representations that are (re)activated by famous faces only (Henson et al., 2000). Interestingly, priming effects and visibility were not found to be significantly dissociated when prime stimuli were rendered invisible by IS. Beyond a mere absence of evidence, this negative finding could be meaningful, as stimulation conditions were perfectly equated between masking and IS (see Materials and Methods). This is notably corroborated by the fact that no observer independently reported the presence of two masking techniques.

A classical pitfall when arguing for the existence of unconscious effects is the possibility that the direct measure (here, objective visibility) is less sensitive than the indirect one (here priming). If this were the case in our experiment (due to unaccounted-for differences in task difficulty, or memory) priming could mistakenly be attributed to unconscious processes in conditions where objective visibility does not deviate from chance, while actually arising from isolated trials in which the prime stimulus was at least partly visible. We anticipated this issue by combining objective and subjective visibility measures on a trial-by-trial basis. Therefore, we could restrict the analysis of priming effects to those trials in which participants reported having no experience or just a brief glimpse of the prime face. Importantly, observers were asked to report seeing a "brief glimpse" only when they perceived meaningless luminance or contrast patterns (i.e., no facial features). When considering such trials only, performance in the objective visibility task dropped in all mask contrast conditions, although it still deviated significantly from chance in the medium mask contrast condition in Experiment 1, and at the weak mask contrast condition in Experiment 2. Two alternative hypotheses explain this surprising result. The first one is that some subjects performed the subjective visibility task incorrectly, erroneously reporting no experience of the prime's features while consciously seeing some of them. The second one is that subjects genuinely had no experience of the prime's features, but related unconscious representations lead them to still perform higher than chance-level in the objective visibility task. We cannot disentangle these two possibilities. Subjective measures of awareness (like the Perceptual Awareness Scale used here) can be seen as a more sensitive assessment of awareness than objective measures, such as the 2-AFC reported here (Cheesman and Merikle, 1986; Sandberg et al., 2010; see also Sandberg et al. in the current issue for a review of different visibility measures).

Taken together, our results echo, but do not entirely match previous results showing repetition and identity priming for famous but not for unfamiliar faces (Henson et al., 2008; Kouider et al., 2009). Note that in these last two studies, priming effects were possibly driven by residual visibility, as no trial-by-trial subjective visibility measure was performed [the authors relied instead on linear regression analyses as advocated by Greenwald et al. (1995) to claim unconscious priming, see **Figure 2** in Henson et al., 2008 and **Figure 1** in Kouider et al., 2009]. Regardless, our findings support the conclusion that the processing of facial identity (for faces previously known to the subject) can occur when stimulus awareness is prevented by masking.

The absence of identity priming under IS is in line with several studies that failed to demonstrate high-level face processing under IS at the behavioral level (see Faivre et al., 2014, in the current issue for a review). Although not reaching significance in the Null Hypothesis Significance Testing (NHST) framework commonly used in psychology (see recent discussions in the literature on replicability and the pitfalls of NHST, e.g., Cumming, 2013), one cannot help but notice that the mean priming effects we measured for the middle mask contrast under IS are positive; however, they show much greater inter-subject variability than in masking. This may reflect a situation where priming does occur for some subjects, which is in and of itself a finding worth pursuing further: IS may not be equally effective for all subjects, owing to individual differences in the combination of information from the two eyes (which is not involved in masking).

The absence of an unconscious repetition priming effect under IS is a bit surprising, as it was previously reported by at least two studies (Barbot and Kouider, 2011; Stein et al., 2013). In addition, it was shown that the similarity between two stimuli differing only by size (generally 20%, as in our repetition priming procedure) can be captured as early as the primary visual cortex (Faivre and Koch, 2014). We expected this similarity to potentially drive repetition priming under IS, which fell short of significance at the lowest mask contrast ($p = 0.13$). The absence of priming here may be attributed to the fact that our stimuli were very carefully equated in terms of low-level visual properties (a Gaussian mask removed peripheral facial features such as hair and ears as well as the background; faces were carefully aligned and matched for shape; image histograms were equated), which was not the case in previous studies. In addition, the absence of a significant effect may stem from the relatively smaller number of subjects, and fewer trials per subject that we collected in Experiment 1, hence making Experiment 1 (more) underpowered. This is because we were expecting to find strong effects in the repetition priming experiment and focused our resources on the identity priming (different viewpoint) experiment.

In our efforts to equate masking and IS we had to strip the latter down to a lesser version of what it really is. The decision to use one or the other technique is usually dictated by the duration of the stimulus that the researcher wishes to mask. If the researcher plans to mask a stimulus longer than about 50ms, then the combination of forward and backward masking becomes less effective and Continuous Flash Suppression (Tsuchiya and Koch, 2005) is usually preferred. For a fair comparison with masking, we are therefore limited to presentation time of the stimulus to 50 ms in IS (which we see as a lesser form of CFS). Under these brief presentation times, we found that face processing was qualitatively more disrupted than with masking, making a point on how the two techniques differ in their mechanisms and behavioral consequences. However, our data does not pertain to whether longer invisible stimulus durations as typically used with CFS would allow for higher level processing of faces, as previous reports have claimed. In the future, one could extend the comparison we performed to conditions of longer stimulus duration, for example using a modified version of masking allowing for longer (but still discontinuous) suppression periods like the standing wave of invisibility (Macknik and Livingstone, 1998).

We want to emphasize the potential importance of small, apparently harmless variations in experimental design. Here for instance, primes were clearly visible in as many as one third of the trials at the lowest mask contrast. Does intermixing visible trials with invisible trials influence the unconscious processing of invisible primes by changing subject's attention and expectations? Does the proportion of these visible trials matter? Further experiments would be needed to assess this empirically. While we report effects that paint masking as allowing more and higher level processing of masked stimuli than IS, we do not know whether these effects would hold if primes were invisible in all trials. Perhaps this is one source of the differences between our study and previous results on face identity priming (Henson et al., 2008; Kouider et al., 2009). Such idiosyncrasies that are difficult to faithfully adhere to when replicating an experiment from a published paper are the main reason why comparing different suppression techniques should be done in the context of a single experiment, in the hands of the same researcher, equating all parameters that can be equated. We encourage other researchers to conduct such controlled studies and are hopeful that a better understanding of unconscious processing, and guidelines on which technique is appropriate to disrupt which level of processing, will emerge from such an effort.

ACKNOWLEDGMENTS

This research, and Julien Dubois, were supported by the G. Harold and Leila Y. Mathers Charitable Foundation, Nathan Faivre by the Fyssen Foundation, Gregory Izatt by a Summer Undergraduate Research Fellowship from the California Institute of Technology. The authors are very grateful to Hagar Gelbard-Sagiv for providing some of the face images used in our experiments.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fpsyg.2014.00659/abstract

REFERENCES

Almeida, J., Mahon, B. Z., and Caramazza, A. (2010). The role of the dorsal visual processing stream in tool identification. *Psychol. Sci.* 21, 772–778. doi: 10.1177/0956797610371343

Almeida, J., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proc. Natl. Acad. Sci.* 105, 15214–15218. doi: 10.1073/pnas.0805867105

Almeida, J., Pajtas, P. E., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2013). Affect of the unconscious: visually suppressed angry faces modulate our decisions. *Cogn. Affect. Behav. Neurosci.* 13, 94–101. doi: 10.3758/s13415-012-0133-7

Barbot, A., and Kouider, S. (2011). Longer is not better: nonconscious overstimulation reverses priming influences under interocular suppression. *Atten. Percept. Psychophys.* 74, 174–184. doi: 10.3758/s13414-011-0226-3

Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., and Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 4783–4788. doi: 10.1073/pnas.0509634103

Brainard, D. H. (1997). The psychophysics toolbox. *Proc. Natl. Acad. Sci. U.S.A.* 10, 433–436.

Breitmeyer, B., and Ogmen, H. (2006). *Visual Masking: Time Slices Through Conscious and Unconscious Vision,* Vol. 41. New York, NY: Oxford University Press.

Cheesman, J., and Merikle, P. M. (1986). Distinguishing conscious from unconscious perceptual processes. *Can. J. Psychol.* 40, 343–367. doi: 10.1037/h0080103

Cumming, G. (2013). The new statistics: why and how. *Psychol. Sci.* 25, 7–29. doi: 10.1177/0956797613504966

Damien, M. F. (2001). Congruity effects evoked by subliminally presented primes: automaticity rather than semantic processing. *J. Exp. Psychol. Hum. Percept. Perform.* 27, 154–165. doi: 10.1037/0096-1523.27.1.154

Faivre, N., Berthet, V., and Kouider, S. (2012). Nonconscious influences from emotional faces: a comparison of visual crowding, masking, and continuous flash suppression. *Front. Psychol.* 3:129. doi: 10.3389/fpsyg.2012.00129

Faivre, N., Berthet, V., and Kouider, S. (2014). Sustained invisibility through crowding and continuous flash suppression: a comparative review. *Front. Psychol.* 5:475. doi: 10.3389/fpsyg.2014.00475

Faivre, N., and Koch, C. (2014). Inferring the direction of implied motion depends on visual awareness. *J. Vis.* 14:4. doi: 10.1167/14.4.4

Greenwald, A. G., Klinger, M. R., and Schuh, E. S. (1995). Activation by marginally perceptible ("subliminal") stimuli: dissociation of unconscious from conscious cognition. *J. Exp. Psychol. Gen.* 124, 22–42. doi: 10.1037/0096-3445.124.1.22

Henson, R., Shallice, T., and Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science* 287, 1269–1272 doi: 10.1126/science.287.5456.1269

Henson, R. N., Mouchlianitis, E., Matthews, W. J., and Kouider, S. (2008). Electrophysiological correlates of masked face priming. *Neuroimage* 40, 884–895. doi: 10.1016/j.neuroimage.2007.12.003

Kanai, R., Bahrami, B., and Rees, G. (2010). Human parietal cortex structure predicts individual differences in perceptual rivalry. *Curr. Biol.* 20, 1626–1630. doi: 10.1016/j.cub.2010.07.027

Kiesel, A., Kunde, W., and Hoffmann, J. (2007). Mechanisms of subliminal response priming. *Adv. Cogn. Psychol.* 3, 307. doi: 10.2478/v10053-008-0032-1

Kim, C., and Blake, R. (2005). Psychophysical magic: rendering the visible "invisible." *Trends Cogn. Sci.* 9, 381–388. doi: 10.1016/j.tics.2005.06.012

Kleiner, M., Brainard, D., and Pelli, D. (2007). "What's new in Psychtoolbox-3?" *Perception* 36, ECVP Abstract Supplement. doi: 10.1068/v070821. Available online at: http://psychtoolbox.org/PsychtoolboxCredits

Kouider, S., and Dehaene, S. (2007). Levels of processing during non-conscious perception: a critical review of visual masking. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 363, 857–875. doi: 10.1098/rstb.2007.2093

Kouider, S., Eger, E., Dolan, R., and Henson, R. N. (2009). Activity in face-responsive brain regions is modulated by invisible, attended faces: evidence from masked priming. *Cereb. Cortex* 19, 13–23. doi: 10.1093/cercor/bhn048

Lin, Z., and He, S. (2009). Seeing the invisible: the scope and limits of unconscious processing in binocular rivalry. *Prog. Neurobiol.* 87, 195–211. doi: 10.1016/j.pneurobio.2008.09.002

Macknik, S. L., and Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual system. *Nat. Neurosci.* 1, 144–149. doi: 10.1038/393

Moradi, F., Koch, C., and Shimojo, S. (2005). Face adaptation depends on seeing the face. *Neuron* 45, 169–175. doi: 10.1016/j.neuron.2004.12.018

Pelli, D. (1997). The videotoolbox software for visual psychophysics: transforming numbers into movies. *Spat. Vis.* 10, 437–442. doi: 10.1163/156856897X00366

Ramsøy, T., and Overgaard, M. (2004). Introspection and subliminal perception. *Phenomen. Cogn. Sci.* 3, 1–23. doi: 10.1023/B:PHEN.0000041900.30172.e8

Sandberg, K., Timmermans, B., Overgaard, M., and Cleeremans, A. (2010). Measuring consciousness: is one measure better than the other? *Conscious. Cogn.* 19, 1069–1078. doi: 10.1016/j.concog.2009.12.013

Stein, T., Seymour, K., Hebart, M. N., and Sterzer, P. (2013). Rapid fear detection relies on high spatial frequencies. *Psychol. Sci.* 25, 566–574. doi: 10.1177/0956797613512509

Tong, F., Meng, M., and Blake, R. (2006). Neural bases of binocular rivalry. *Trends Cogn. Sci.* 10, 502–511. doi: 10.1016/j.tics.2006.09.003

Tsuchiya, K., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Whelan, R. (2008). Effective analysis of reaction time data. *Psychol. Rec.* 58, 475–482.

Willenbockel, V., Sadr, J., Fiset, D., Horne, G., Gosselin, F., and Tanaka, J. (2010). The shine toolbox for controlling low-level image properties. *J. Vis.* 10, 7–653. doi: 10.1167/10.7.653

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 09 April 2014; accepted: 09 June 2014; published online: 07 July 2014.
Citation: Izatt G, Dubois J, Faivre N and Koch C (2014) A direct comparison of unconscious face processing under masking and interocular suppression. Front. Psychol. ***5****:659. doi: 10.3389/fpsyg.2014.00659*
This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 16 June 2014
doi: 10.3389/fpsyg.2014.00601

Unconscious neural processing differs with method used to render stimuli invisible

Sergey V. Fogelson[1]*, **Peter J. Kohler**[2], **Kevin J. Miller**[3], **Richard Granger**[1] and **Peter U. Tse**[1]

[1] Department of Psychological and Brain Sciences, Dartmouth College, Hanover, NH, USA
[2] Department of Psychology, Stanford University, Stanford, CA, USA
[3] Princeton Neuroscience Institute, Princeton University, Princeton, NJ, USA

Edited by:
Julien Dubois, California Institute of Technology, USA

Reviewed by:
Guido Hesselmann, Charité Campus Mitte, Germany
Radoslaw Martin Cichy, MIT, USA

***Correspondence:**
Sergey V. Fogelson, Department of Psychological and Brain Sciences, Dartmouth College, H.B. 6207 Moore Hall, Hanover, NH 03755, USA
e-mail: sergeyfogelson@gmail.com

Visual stimuli can be kept from awareness using various methods. The extent of processing that a given stimulus receives in the absence of awareness is typically used to make claims about the role of consciousness more generally. The neural processing elicited by a stimulus, however, may also depend on the method used to keep it from awareness, and not only on whether the stimulus reaches awareness. Here we report that the method used to render an image invisible has a dramatic effect on how category information about the unseen stimulus is encoded across the human brain. We collected fMRI data while subjects viewed images of faces and tools, that were rendered invisible using either continuous flash suppression (CFS) or chromatic flicker fusion (CFF). In a third condition, we presented the same images under normal fully visible viewing conditions. We found that category information about visible images could be extracted from patterns of fMRI responses throughout areas of neocortex known to be involved in face or tool processing. However, category information about stimuli kept from awareness using CFS could be recovered exclusively within occipital cortex, whereas information about stimuli kept from awareness using CFF was also decodable within temporal and frontal regions. We conclude that unconsciously presented objects are processed differently depending on how they are rendered subjectively invisible. Caution should therefore be used in making generalizations on the basis of any one method about the neural basis of consciousness or the extent of information processing without consciousness.

Keywords: continuous flash-induced suppression, flicker fusion, fMRI, categorical representation, multi-voxel pattern analysis, consciousness

INTRODUCTION

Blindsight (Weiskrantz, 1990) reveals that some patients who lack conscious vision can have residual unconscious processing. A similar state of affairs can be achieved with normal subjects when stimuli are presented in ways that restrict objects from reaching awareness. Since at least the time of the earliest studies on subliminal perception (Peirce and Jastrow, 1884), researchers have investigated the extent of neural processing that occurs when stimuli are rendered invisible to an observer. This work has stimulated the discovery of multiple ways of eliminating a stimulus from awareness, each with its own specific methodological advantages and disadvantages.

Forward and backward masking allow a stimulus to be rendered subjectively invisible by briefly presenting other highly salient stimuli just before or after the to-be-masked stimulus. Although this method is very effective at rendering a stimulus invisible, the stimulus of interest can be presented for only very brief (<100 ms) durations (Macknik, 2006). Binocular rivalry allows for longer durations of stimulus invisibility by presenting a different stimulus to each eye. Typically, only one eye's input is seen at a time, rendering input to the other eye invisible (Blake, 2001). Although this method extends the duration of stimulus invisibility, stimulus visibility varies stochastically, making both its onset and duration unpredictable (Blake et al., 1971).

A recent elaboration of the binocular rivalry technique, called "continuous flash suppression" (CFS) (Fang and He, 2005; Tsuchiya and Koch, 2005; Koch and Tsuchiya, 2007), presents a temporally dynamic high-contrast image sequence to one eye, while the stimulus of interest is presented to the other eye. This largely removes the unpredictability of standard binocular rivalry between static images, because the dynamic stimulus is so salient that it completely dominates perception in most cases; subjects rarely report seeing the other stimulus at all. This also means that the duration of invisibility can be extended substantially, sometimes for as long as several minutes (Tsuchiya and Koch, 2005). Both binocular rivalry and CFS, however, rely on presenting a stimulus of non-interest to one eye, which might not always be desirable, especially with CFS where this stimulus needs to be highly salient.

This can be avoided by using dichoptic color masking, which involves showing isoluminant, oppositely colored versions of the *same* stimulus to each eye (Moutoussis and Zeki, 2002; Schurger et al., 2010). The disadvantage of this method is that images must be low-contrast and low-spatial frequency to effectively render the stimulus of interest invisible (Schurger et al., 2010). In a modification of this technique (Hoshiyama et al., 2006), which we will refer to as "chromatic flicker fusion" (CFF), two isoluminant, oppositely colored stimuli are simultaneously presented to both eyes, one image at a time, at a temporal frequency above the flicker fusion threshold (~30 Hz). The two images will fuse together such that the image is perceived to be uniformly colored and unchanging (Hecht and Verrijp, 1933). This allows stimuli of higher contrast and higher spatial frequency to be displayed, with the additional advantage that the stimulus of interest is displayed continuously to both eyes.

Although each of the aforementioned methods effectively renders a stimulus invisible to the observer, this is accomplished in profoundly different ways. To the best of our knowledge, the possibility that different methods of rendering a stimulus invisible can lead to differential residual neural processing in the absence of awareness has only been addressed to a limited extent, and only in rhesus macaques, in the literature (Macknik and Livingstone, 1998), and work in humans has only addressed behavioral differences between distinct stimulus invisibility-inducing paradigms (Faivre et al., 2012). Here we use two of these methods, CFS and CFF, to render identical stimuli from two distinct categories (faces and tools) invisible in human beings, and address the possibility of their differential neural processing. Both methods have been shown to allow residual neural processing of stimuli that are invisible to the observer, and are equally effective at rendering relatively high contrast and high spatial frequency stimuli invisible for several seconds or longer (Fang and He, 2005; Jiang et al., 2007; Sterzer et al., 2008).

Multivariate pattern analysis (MVPA) can be used to evaluate the extent to which stimulus information can be recovered from functional neuroimaging data (Cox and Savoy, 2003). We used MVPA to determine whether stimulus category information (in our case, faces or tools) was present in anatomical regions throughout the brain across our three presentation methods (visible, invisible during CFF, and invisible during CFS). If stimulus category can be recovered in a brain region under one presentation condition, but not another, this would suggest that the two conditions lead to differential neural processing in that region. Thus, identifying regions that contain stimulus information under one condition, but not another, allows for the discovery of potential differences in the unconscious processing elicited by different presentation methods.

We were also able to look within areas where classification was in fact possible with more than one presentation method and ask the additional question of whether there were commonalities in the representations of category information elicited by visible and both invisible presentation methods. To accomplish this, we used a cross-method classification approach and tested whether a pattern classifier trained on data from one presentation method could successfully predict stimulus category in a test dataset from the other presentation method. Successful cross-method classification may indicate that different presentation methods yield dissociable representations within the same brain region.

Several experimental outcomes are possible. It could be that stimuli are processed in the same way, regardless of how they are rendered invisible. This would be the case if a single, presumably cortical, bottleneck for conscious visual processing exists, beyond which there is no processing of unconscious stimuli. In this case we would expect category information to be present in largely the same subset of brain areas regardless of the method used to render the stimuli invisible. On the other hand, if unconscious processing depends on how the stimuli are rendered invisible, we would expect to see areas where one method allows classification, but the other does not, and other areas where the opposite is the case. Such a result would suggest that properties of the method used to induce stimulus invisibility had a significant effect on the propagation of stimulus information through cortex.

We collected full-brain fMRI data while presenting subjects with pictures of faces and tools under three conditions (visible, invisible during CFS, invisible during CFF). We found that the cortical and subcortical areas that distinguish between unconsciously processed face and tool categories were largely nonoverlapping between the CFS and CFF conditions. Although visible stimulus category information was present throughout cortex, stimulus information rendered invisible via CFS was recoverable exclusively from occipital cortex, whereas stimulus information rendered invisible via CFF was recoverable from occipital, temporal, and frontal regions. These results suggest that invisible objects are processed differently depending on the method used to render them invisible.

MATERIALS AND METHODS

PARTICIPANTS

Seventeen healthy subjects (9 men) aged between 19 and 29 (mean age 24.3 years) participated in the experiment. All subjects had normal or corrected-to-normal vision and gave written, informed consent in accordance with procedures and protocols for testing human subjects, approved by the Institutional Review Board of Dartmouth College.

EXPERIMENTAL DESIGN

Stimuli were human faces (2 male, 2 female) and common tools (spoon, fork, hammer, wrench) drawn as either red or green outlines on a yellow-green background. Faces subtended approximately 4.5° by 8° of visual angle, whereas tool stimuli were ~2.5° by ~8° and were always elongated along the vertical axis (Sakuraba et al., 2012). All images were presented within an 8° by 8° viewing window. Additionally, each image contained a central white fixation cross that subtended 0.75° by 0.75° of visual angle. Stimuli were always presented for 2 s during a given trial, regardless of trial type.

We used two methods to render face and tool stimuli invisible to subjects. During CFF, subjects were presented with two isoluminant oppositely colored (red and green) images that flickered dynamically in counter-phase with each other at 30 Hz. Since the flicker rate is above the critical flicker fusion threshold for color (Jiang et al., 2007), this manipulation led subjects to perceive a continuous uniform dark-green colored field, with a white fixation cross in the center (**Figure 1**). Previous results show that this method is effective at rendering stimuli invisible, while still allowing unconscious processing (Moutoussis and Zeki, 2002; Jiang et al., 2007). In order to ensure that the values of green and red used for the CFF stimuli were isoluminant so that they could support fusion, they were adjusted prior to the experiment to be perceptually isoluminant for each subject individually. This isoluminance task was performed using heterochromatic flicker photometry with alternating red and green squares (Ives, 1911; Lee et al., 1988). During this calibration task, subjects saw a single square that rapidly flickered (20 Hz) between red and green; they then had to adjust the luminance of the green color until the magnitude of flickering between the two colors was perceptually minimized. At the minimal flicker point, subjects perceived a uniform, minimally flickering square with a color approximately halfway between the two original colors (a dark greenish yellow color). Once this value was determined, all stimuli used for each subject across all presentation methods had identical contrast values with the specific luminance values found during calibration.

We contrasted this method with CFS, which has regularly been shown to render a large variety of stimulus types invisible to the observer (Koch and Tsuchiya, 2007), evident in both behavioral (Tsuchiya and Koch, 2005; Almeida et al., 2008; Bahrami et al., 2010) and neuroimaging data (Fang and He, 2005; Jiang and He, 2006; Sterzer et al., 2008). We presented a high-contrast dynamically changing (10 Hz) "Mondrian" pattern, consisting of randomly positioned rectangles of various sizes and colors, in each subject's dominant eye, and showed isoluminant red/green face or tool stimuli identical to those used for the CFF condition to the non-dominant eye. This rendered the stimulus presented to the non-dominant eye invisible (**Figure 1**). A white fixation cross, identical to that used in the CFF condition, was placed on top of each Mondrian stimulus. Both of these manipulations rendered faces and tools invisible and allowed us to use fMRI to investigate cortical and subcortical object processing in the absence of awareness. For comparison, we also measured patterns of activity when subjects were presented with only one of the two CFF stimuli (red or green), without any flicker, which rendered the stimuli fully visible.

DATA ACQUISITION

Structural and functional data were collected using a Philips 3T Achieva scanner with a 32-channel head coil. BOLD signals were measured with an EPI (echo-planar imaging) sequence [35 axially oriented slices, 3.0 × 3.0 mm in-plane voxel resolution, 3.5 mm slice thickness, no gap, interleaved slice acquisition, FOV = 240 × 240 × 122, TE = 35 ms, flip angle = 90°, TR = 2000 ms, acquired matrix size = 80 × 80, reconstructed matrix size = 80 × 80, P reduction (RL) sense factor of 2, S reduction (FH) sense factor of 1] and structural anatomical scans were acquired using an MPRAGE sequence (220 axial slices, 0.94 × 0.94 mm in-plane voxel resolution, 1 mm slice thickness, acquired matrix size = 240 × 187, reconstructed matrix size = 256 × 256, FOV = 240 × 188 × 220, TR/TE = 8.2/3.7). Inside the scanner bore, subjects viewed stimuli through MR-compatible VisuaStimDigital binocular presentation goggles (Resonance Technology Inc., Los Angeles, CA). We used a slow event related design where each 2 s trial was followed by a 6 or 8 s blank ISI with a fixation cross (both ISIs had an equal probability of occurring and one was randomly chosen following each trial). All 8 stimuli were shown twice per run using each experimental method (fully visible, CFF, CFS). For the visible and CFS conditions one of the two presentations of each stimuli utilized the green outline CFF stimulus, and the other presentation utilized the red outline CFF stimulus, while during the CFF condition both presentations of each were identical (red and green outline flickering). This gave a total of 48 stimuli per run (8 stimuli × 2 different color outlines × 3 presentation methods). Trials for CFS, CFF, and visible conditions occurred in random order throughout each experimental run. A near-optimal run order was generated by creating millions of possible run orders and evaluating them according to first and second-order correlations in the stimulus order at the category level (so that the probability that a face followed a face or a tool followed a tool was minimized) and selecting the order with the minimum first and second-order correlation (for a first-order correlation, this makes the probability that a face followed a tool roughly the same as the probability that it would follow a face; for a second-order correlation, this made it so that the probability of a face followed by either a face or a tool and again followed by a face is roughly the same as the probability that the second succeeding stimulus is a tool). Stimulus orders were generated on a per-subject basis, such that each subject saw a different first-order and second-order correlation-minimized ordering of images. Following each presentation, subjects indicated stimulus category with one button box, guessing in the cases where they had no awareness of the stimulus. Using a second button box, subjects were also asked to indicate whether stimulus breakthrough occurred (that is, whether they saw anything other than a Mondrian pattern or a uniformly colored field). During visible trials, subjects were required to use this second button box to indicate that a stimulus was clearly visible.

Experimental runs lasted for 242 2-s TRs (484 s). All subjects underwent 8 experimental runs acquired in a single scanning session. Any CFS or CFF trials during which subjects indicated that breakthrough had occurred were eliminated from further analysis. To further ensure that stimuli were indeed completely invisible to subjects during unconscious trials, any experimental runs for which subjects were able to guess the category of invisible stimuli with greater than 75% accuracy (cumulative binomial $p < 0.05$) were not used in further analyses for that trial type. The 75% criterion was chosen to exclude runs where button presses during unconscious trials could be used to decode stimulus category with greater than chance accuracy. This occurred quite rarely (three runs for three different subjects, out of a total of 136 runs of data gathered across all subjects). All fully visible trials were included, regardless of subject response.

DATA PREPROCESSING

Functional imaging data were preprocessed using FSL (Jenkinson et al., 2011). Preprocessing included motion correction, high pass filtering (>0.01 Hz) and spatial smoothing with a 5 mm Gaussian kernel. After preprocessing, multi-voxel pattern analysis was performed on the data with a linear support vector machine (SVM) pattern classifier as implemented in PyMVPA (Hanke et al., 2009) using all default parameters (see Within-method and cross-method category classification). Data from the second and third TR (4 and 6 s) following stimulus onset were

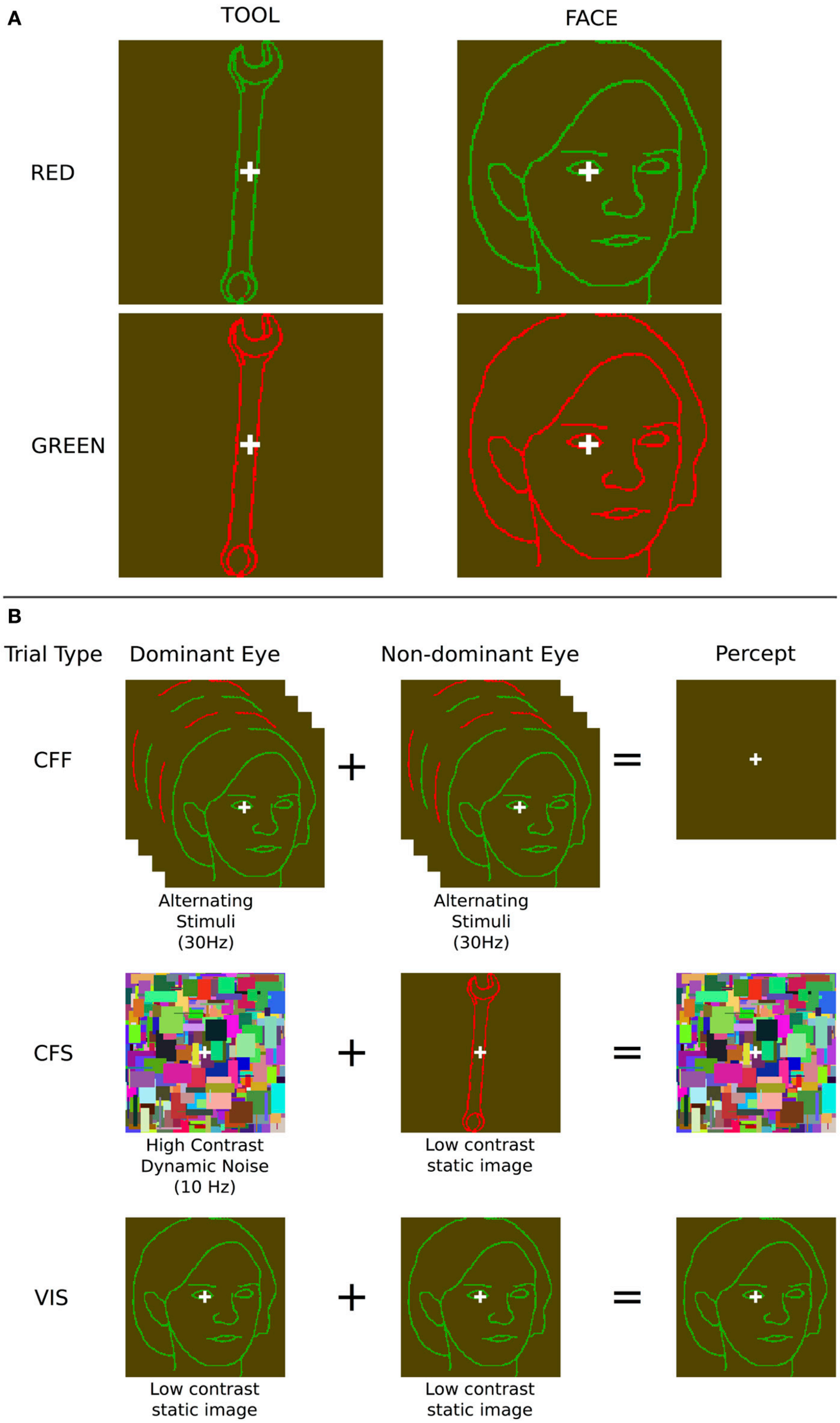


FIGURE 1 | Stimuli and presentation methods used. (A) Example face and tool stimuli—note that the contrast of the outline stimuli, which were in fact perceptually isoluminant, is enhanced here for illustration purposes. **(B)** The three presentation methods: During chromatic flicker fusion trials, isoluminant images were flickered in both eyes continuously at 30 Hz and rendered invisible; During continuous flash suppression trials, an object image was presented to the non-dominant eye and a high contrast pattern changing at 10 Hz was presented to the dominant eye, rendering the object image invisible; During visible trials, identical object images were presented to both eyes. During all trials, image visibility was tested using objective behavioral measurements.

used for classification. All trials within a run were averaged to create a single pattern of activity per category per run.

All individual ROI masks were generated using FreeSurfer's automatic anatomical parcellations of both cortical gray-matter and subcortical regions (Destrieux et al., 2010), allowing us to perform the analyses within each subject's own anatomical space and to avoid the loss of statistical power and normalization inaccuracies associated with group-level analyses done in a standard space. For a given anatomical region, masks from both hemispheres were combined to yield a single bilateral ROI. This yielded a total of 67 bilateral ROIs per subject. A cortical surface reconstruction of a standard anatomical template (the MNI 152-brain average atlas) was also created using SUMA (Saad and Reynolds, 2012) for illustrating group-level ROI results.

WITHIN-METHOD AND CROSS-METHOD CATEGORY CLASSIFICATION

All analyses were performed in each subject's native space using the bilateral anatomically defined regions of interest (ROI) described above. All pattern classifications where performed using a linear SVM classifier, as described above. First, classification of faces and tools was performed using only the data acquired during the visible presentation method. This was done in order to identify the set of areas that contained visible categorical information, and to limit the number of comparisons performed when analyzing the conditions where there was no awareness (that is, during either CFF or CFS trials). The assumption was that areas where categorical information was present in the visible case would make the best candidates for investigating the presence of information in the absence of visual awareness. All classifications were performed using leave-one-run-out cross-validation and the resulting d-prime values across all subjects were compared with chance accuracy using a one-sided t-test. The resulting p-values (during the visible case) were then corrected for multiple comparisons using False Discovery Rate (FDR) to get corrected p-values. Those ROIs that survived this initial correction (corrected $p < 0.05$) were then explored in an exactly analogous manner using the data acquired during the two invisible presentation methods (CFF and CFS). Furthermore, paired t-tests comparing each display method were also performed in those cases where significant classification occurred. In order to ensure that actual categorical information was being captured for all three conditions, we did the classification such that there was no overlap at the individual-exemplar level between the trials used for the training and test data sets given to the classifier. Specifically, we split each run so that we trained the classifier on one specific set of exemplars across all but one run, and then tested on the left-out exemplars for the held-out run. This same method was repeated on the other set of exemplars (that which was not used for training), with testing happening on the remaining (not trained exemplars) with the same kind of run splits (all but one run training, held out run for testing). This was done for every possible combination of training and testing runs. The two kinds of cross-validation were then averaged together to come up with a single averaged cross-validated cross-exemplar d-prime value. If there were not at least two usable exemplars within a run for a given presentation method, that run was thrown out from analysis for that presentation method (this was only done for 4 functional runs across all 18 subjects). Splitting the data in this way forced the classifier to use voxel patterns that were at least somewhat removed from the most simple low-level identifying features of the stimuli.

In addition, three different kinds of cross-method classification analyses were performed: (1) between invisible presentation methods, (2) invisible to visible, and (3) visible to invisible. As was the case with the within-method classification, cross-method classification was limited to those ROIs that were significant (after FDR-correction) in the visible case. Again, results were FDR-corrected across ROIs and within each analysis. The "between invisible" classification tested whether any regions were capable of distinguishing invisible faces from invisible tools when a classifier was trained on one of the methods (CFF or CFS) and tested on a held-out run that included only trials from the other method (CFS or CFF, respectively). In the "invisible to visible" classification, we trained the classifier on trials from one of the invisible methods (CFF or CFS) and attempted to classify the category (face or tool) during a visible presentation within a given ROI. In "visible to invisible" classification, the approach was exactly the same, except the training and testing patterns were swapped (training was performed on visible trials and testing was performed on one of the invisible methods).

RESULTS

BEHAVIORAL RESULTS

Behavioral data collected during scanning show that subjects were at chance when guessing stimulus category during both invisible conditions (mean accuracy across all trials and subjects for CFS: 49.7%, $p = 0.9$; and CFF: 49.4%, $p = 0.29$, one-sided t-test against chance accuracy) and at ceiling (99.4%, $p < 0.0001$, one-sided t-test against chance accuracy) during the visible condition. Subjects rarely reported seeing the faces or tools during either invisible condition (3.1% of trials for CFS and 4.3% of trials for CFF across all subjects) and almost always saw stimuli presented during the visible condition (96.2% of trials). We conclude that both methods successfully rendered the stimuli completely invisible.

CATEGORY CLASSIFICATION WITHIN EACH PRESENTATION METHOD

In order to identify areas across the entire brain that distinguished faces from tools during the visible case, we used an exhaustive region-of-interest (ROI) approach. Linear SVM classification was performed within 67 anatomically defined bilateral ROIs (see Methods). All reported classification results have been FDR-corrected for multiple comparisons ($p < 0.05$) as described in the methods. Our analysis revealed a subset of occipital, temporal, parietal, and frontal ROIs where multivariate pattern classification could distinguish faces from tools when the stimuli were clearly visible. In occipital cortex, these ROIs included the inferior occipital gyrus and sulcus [$t_{(16)} = 3.21$ $p < 0.05$], middle occipital gyrus [$t_{(16)} = 3.21$, $p < 0.05$], lingual gyrus [$t_{(16)} = 2.37$, $p < 0.05$], occipital pole [$t_{(16)} = 2.81$, $p < 0.05$], middle and lunate sulci [$t_{(16)} = 2.79$, $p < 0.05$], and the anterior occipital sulcus [$t_{(16)} = 2.45$, $p < 0.05$] (see **Figure 2**). In temporal cortex, these included the fusiform gyrus [$t_{(16)} = 3.35$, $p < 0.05$], posterior transverse collateral sulcus [$t_{(16)} = 2.89$, $p < 0.05$], and

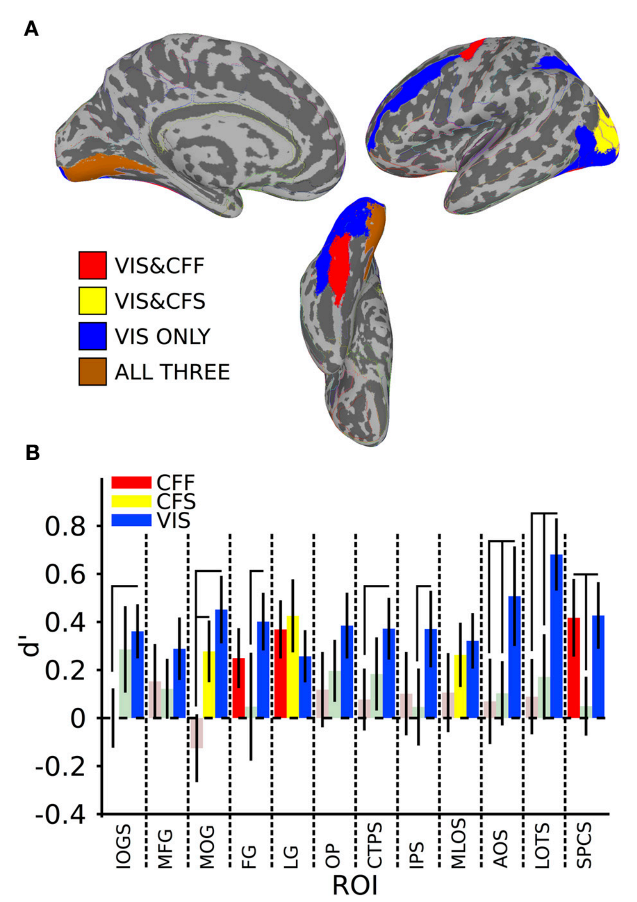


FIGURE 2 | Within-method classification results. (A) Colored anatomical ROIs indicate regions where classification of stimulus category was significantly above-change ($p < 0.05$ FDR-corrected) for each presentation method. **(B)** Bar graphs showing the classification accuracy for each method within all ROIs where above-chance classification was possible for the visible presentation method. Saturated (yellow, blue, and red) colors indicate significant classification, whereas desaturated (light red, light green) colors indicate non-significant classification. Full region names for the ROI abbreviations can be found in **Table 1**.

the lateral occipitotemporal sulcus [$t_{(16)} = 4.54, p < 0.05$]. Three additional ROIs outside of occipitotemporal cortex were also identified as containing patterns that could reliably distinguish visible faces from tools: the intraparietal sulcus [$t_{(16)} = 2.33$, $p < 0.05$], the superior part of the precentral gyrus [$t_{(16)} = 3.08$, $p < 0.05$], and the middle frontal gyrus [$t_{(16)} = 2.22$, $p < 0.05$] (see **Figure 2**).

A subset of these regions also showed significant category classification in the absence of stimulus awareness. Categorical classification was possible when subjects were shown CFS-masked images in the middle occipital gyrus [$t_{(16)} = 2.16, p < 0.05$], the middle occipital and lunate sulci [$t_{(16)} = 2.00, p < 0.05$], and in the lingual gyrus [$t_{(16)} = 2.80, p < 0.05$]. Categorical classification was also possible when subjects viewed CFF-masked images in the lingual gyrus [$t_{(16)} = 2.01$, $p < 0.05$], as well as in the fusiform gyrus [$t_{(16)} = 3.05$, $p < 0.05$] and in the superior part of the precentral sulcus [$t_{(16)} = 2.58, p < 0.05$] (see **Figure 2**).

In several areas, categorical decoding was significantly more robust when objects were completely visible rather than when they were made consciously invisible using either of the other methods. Visible objects were significantly more decodable than objects presented during CFF in the inferior occipital gyrus [$t_{(16)} = 2.08$, $p < 0.05$], middle occipital gyrus [$t_{(16)} = 3.05, p < 0.05$], posterior transverse collateral sulcus [$t_{(16)} = 2.08$, $p < 0.05$], and the lateral occipitotemporal sulcus [$t_{(16)} = 2.48$, $p < 0.05$]. In a different subset of regions, visible objects were significantly more decodable than objects presented during CFS, specifically, the fusiform gyrus [$t_{(16)} = 1.80$, $p < 0.05$], the intraparietal sulcus [$t_{(16)} = 1.82, p < 0.05$], in the lateral occipitotemporal sulcus [$t_{(16)} = 2.15$, $p < 0.05$], and in the superior part of the precentral sulcus [$t_{(16)} = 2.22, p < 0.05$].

Finally, in several regions, the two methods for rendering stimuli invisible were significantly distinguishable from each other. Thus, CFF-based trial categorical decoding was significantly more robust than CFS-trial categorical decoding in the superior part of the precentral sulcus [$t_{(16)} = 1.99, p < 0.05$]. On the other hand, CFS-trial categorical decoding was significantly more robust than CFF-trial categorical decoding in the middle occipital gyrus.

To summarize, we found a set of regions within the occipital, temporal, parietal, and frontal lobes that could distinguish fMRI voxel patterns of activity for faces from tools when those objects were clearly visible. Within this set of regions, only a single occipital region, the lingual gyrus, showed the presence of categorical information across all three presentation methods: the visible viewing condition and both invisible conditions in which subjects were completely prevented from consciously identifying the category of the presented objects. Furthermore, visible category information was significantly stronger than category information found during either invisible presentation method in several regions, depending on the method: inferior occipital gyrus, middle occipital gyrus, and posterior transverse collateral sulcus for CFF trials, and in the superior part of the precentral sulcus during CFS trials. In the lateral occipitotemporal sulcus, visible category information was significantly stronger than during both invisible presentation methods. Distinct subsets of regions permitted classification of category information in the two invisible cases. When stimuli were rendered invisible using CFF, categorical information was extractable from the fusiform gyrus and from the superior part of the precentral sulcus, however, only in the latter case was the presence of the categorical information significantly more robust than in the CFS case. When CFS was used, categorical information was present exclusively in occipital regions on the lateral occipital surface (middle occipital gyrus and middle occipital and lunate sulci), but was only significantly more robust than during CFF trials in the middle occipital gyrus.

CROSS-METHOD CATEGORY CLASSIFICATION

We also tested whether patterns of activity for faces and tools could be reliably recovered across presentation methods. We found that a subset of the ROIs described in the previous section, were capable of reliably recovering category information across the invisible presentation methods. Several ROIs showed the presence of information that could reliably distinguish the categories when cross-presentation training and

Table 1 | ROI names, *t*-values, and mean accuracies for all significant within-method classifications, *Indicates FDR-corrected $p < 0.05$.

	Full ROI name	CFF mean	CFF *t*-value	CFS mean	CFS *t*-value	VIS mean	VIS *t*-value	Size cm^2
IOGS	Inferior occipital gyrus and sulcus	0	0	0.29	1.59	0.36	3.21*	23.96
MFG	Middle frontal gyrus	0.15	0.98	0.12	0.98	0.29	2.21*	64.96
MOG	Middle occipital gyrus	−0.13	−0.89	0.28	2.16*	0.45	3.21*	33.69
FG	Fusiform gyrus	0.25	2.00*	0.05	0.21	0.40	3.35*	27.08
LG	Lingual gyrus	0.37	3.05*	0.43	2.80*	0.26	2.37*	42.04
OP	Occipital pole	0.12	0.75	0.2	1.52	0.39	2.81*	38.05
CTPS	Posterior transverse collateral sulcus	0.08	0.60	0.18	1.21	0.37	2.90*	8.36
IPS	Intraparietal sulcus	0.1	0.58	0.05	0.29	0.37	2.33*	55.58
MLOS	Middle occipital and lunate sulci	0.11	0.64	0.26	1.97*	0.32	2.79*	17.84
AOS	Anterior occipital sulcus	0.07	0.39	0.1	0.77	0.51	2.45*	13.24
LOTS	Lateral occipitotemporal sulcus	0.08	0.57	0.18	0.96	0.68	4.54*	17.66
SPCS	Precentral sulcus, superior part	0.42	2.58*	0.05	0.40	0.43	3.08*	24.32

*The first column is the abbreviation used for the given area in **Figure 2**. Areas are arranged in the same order as that found in the bar graphs in **Figures 2– 4**.*

testing regimes were performed in either direction [occipital pole: CFS->CFF: $t_{(16)} = 2.59$, $p < 0.05$; CFF->CFS: $t_{(16)} = 3.33$, $p < 0.05$; inferior occipital gyrus and sulcus: CFS->CFF: $t_{(16)} = 3.39$, $p < 0.05$; CFF->CFS: $t_{(16)} = 2.25$, $p < 0.05$; posterior transverse collateral sulcus: CFS->CFF: $t_{(16)} = 3.20$, $p < 0.05$; CFF->CFS: $t_{(16)} = 2.90$, $p < 0.05$]. In two separate occipital ROIs, categories could only be distinguished either when training on CFF and testing on CFS trials [lingual gyrus—$t_{(16)} = 2.19$, $p < 0.05$] or when training on CFS and testing on CFF trials [middle occipital and lunate sulci—$t_{(16)} = 2.21$, $p < 0.05$]. These data are summarized in **Figure 3**; *t*-values and mean accuracies for all significant comparisons can be found in **Table 2**.

In the invisible to visible case, that is, training on trials from either invisible method and testing on only visible trials, we were unable to find any ROIs that could distinguish the stimulus categories reliably. When training on visible trials and testing on invisible trials, however, we found that several occipital and temporal ROIs could distinguish the categories (**Figure 4**; table of *t*-values and mean accuracies for ROIs found in **Table 2**). Training on visible trials and testing on either invisible presentation method yielded significant classification results in the inferior occipital gyrus and sulcus [VIS->CFF: $t_{(16)} = 4.06$, VIS->CFS: $t_{(16)} = 3.64$, both $p < 0.05$], fusiform gyrus [VIS->CFF: $t_{(16)} = 5.29$, VIS->CFS: $t_{(16)} = 3.82$, both $p < 0.05$], posterior transverse collateral sulcus [VIS->CFF: $t_{(16)} = 2.05$, VIS->CFS: $t_{(16)} = 3.84$, both $p < 0.05$], middle occipital and lunate sulci [VIS->CFF: $t_{(16)} = 2.47$, VIS->CFS: $t_{(16)} = 1.90$, both $p < 0.05$], and in the lateral occipitotemporal sulcus [VIS->CFF: $t_{(16)} = 3.46$, VIS->CFS: $t_{(16)} = 2.52$, both $p < 0.05$]. In four other regions, all in the occipital lobes, reliable visible to invisible categorical classification only occurred when the classifier was tested on CFS trials [middle occipital gyrus: VIS->CFF: $t_{(16)} = -0.31$, $p > 0.05$, VIS->CFS: $t_{(16)} = 3.31$, $p < 0.05$; lingual gyrus: VIS->CFF: $t_{(16)} = -0.48$, $p > 0.05$, VIS->CFS: $t_{(16)} = 3.06$, $p < 0.05$; occipital pole: VIS->CFF: $t_{(16)} = 1.31$, $p > 0.05$, VIS->CFS: $t_{(16)} = 2.57$, $p < 0.05$; anterior occipital sulcus: VIS->CFF: $t_{(16)} = -1.79$, $p > 0.05$, VIS->CFS: $t_{(16)} = 2.67$, $p < 0.05$]. For three of these regions, the classifier performed better with CFS test data than with CFF test data [paired *t*-test, middle occipital gyrus: $t_{(16)} = 2.31$, $p < 0.05$; lingual gyrus: $t_{(16)} = 2.11$, $p < 0.05$; anterior occipital sulcus: $t_{(16)} = 3.63$, $p < 0.05$].

In summary, cross-method category classification was possible exclusively in occipitotemporal cortex. No ROIs were capable of distinguishing visible category trials when classifier training occurred using either invisible method and testing was done using fully visible stimuli. Category information was recoverable when training and testing was done on data collected using different invisible presentation methods only within occipital cortex. Several occipitotemporal ROIs could distinguish face-related from tool-related activity when training a classifier on patterns of activity elicited by visible trials and testing the classifier using patterns elicited by either CFS or CFF trials; however, activity in the middle occipital gyrus, lingual gyrus, and anterior occipital sulcus could reliably predict category when classifier testing was done using CFS trials, and was also reliably more robust than when testing on CFF trials.

DISCUSSION

We presented two categories of objects (tools and faces) to subjects while scanning them using fMRI. Objects were rendered invisible using two methods, CFS and CFF, and were also presented during normal viewing. We used MVPA on the fMRI data to identify anatomically defined areas in which patterns of activation elicited by each presentation method allowed us to recover stimulus category information. Even though there were differences at the level of stimuli when presenting categories using CFS and CFF, there were no differences in the set of face or tool images made invisible using either method. Moreover, we did not classify brain activity by method, but rather by stimulus category. Thus, stimulus differences were orthogonal to our comparisons, and cannot account for our results. Here we show that distinct cortical regions carry information about visual categories when visibility is eliminated by each of these two methods. This result confirms previous findings that neural information processing can occur when stimulus awareness is obstructed by

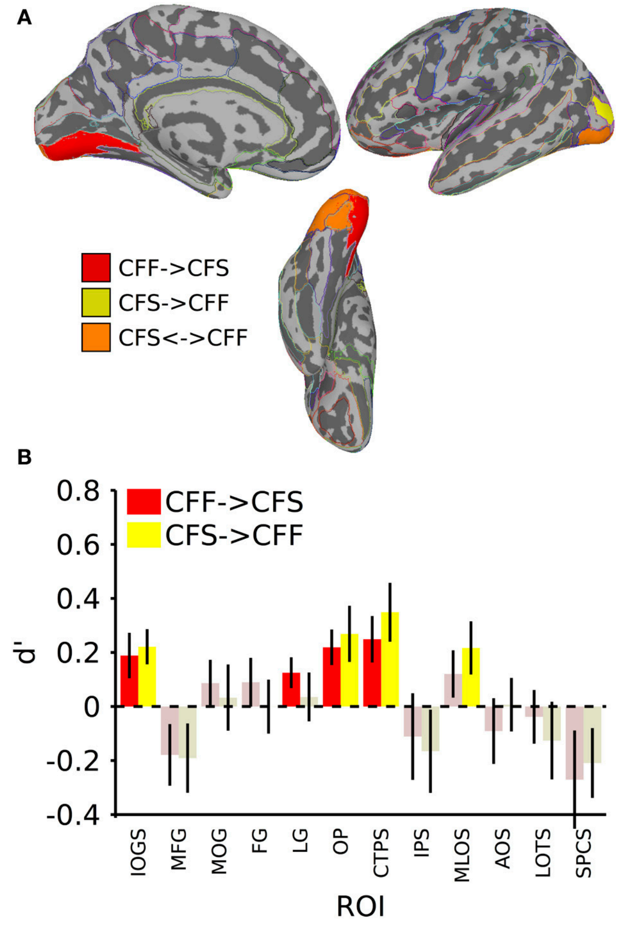


FIGURE 3 | Results for classification across invisible presentation methods. (A) Colored anatomical ROIs indicate regions where category classification was significantly above-chance ($p < 0.05$ FDR-corrected) when performing cross-method category classification between the invisible methods (CFF and CFS). **(B)** Bar graphs of all regions where significant cross-method category classification was possible. Full region names for the ROI abbreviations can be found in **Table 2**. Saturated (yellow and red) colors indicate significant classification, whereas desaturated (light red, light green) colors indicate non-significant classification.

both CFS and CFF (Fang and He, 2005; Jiang et al., 2007; Sterzer et al., 2008), and shows for the first time, that these two different methods for rendering stimuli invisible can activate different, largely non-overlapping, cortical areas. This suggests that cortical representations at the level of categories vary with presentation method.

Our visible classification results identified a neocortical network of occipitotemporal, parietal, and lateral frontal regions that could reliably distinguish faces from tools when the objects were presented under normal viewing conditions and were clearly visible. In several of these regions, not only were the results significant, but they were also significantly stronger than during either invisible case. These results are unsurprising and broadly consistent with previous research. Lateral occipital and superior parietal cortex have both been shown to activate strongly to tools (Vingerhoets et al., 2009; Mahon et al., 2010) and inanimate object stimuli more generally (Chao et al., 1999). Our finding that visible face and tool stimuli can be reliably distinguished from each other in medial and lateral occipitotemporal cortical ROIs, as well as in the intraparietal sulcus, is consistent with these results. A large amount of evidence also suggests that faces robustly activate lateral fusiform regions in the temporal cortex, among other regions (Haxby et al., 2000). Our visible classification results in the middle frontal gyrus show the presence of categorical information outside of these regions, specifically in the middle frontal gyrus and in the superior part of the precentral sulcus.

The category classification results when subjects were not aware of the stimuli are more interesting. When stimuli were suppressed using CFS, category could be recovered exclusively from parts of the occipital lobes, but when CFF was used to keep stimuli from awareness, category information could be recovered from medial occipital, lateral temporal, and lateral frontal cortex. In addition, for both invisible presentation methods, at least one region was found that showed the presence of stronger categorical information than the other invisible presentation method. The only region that could reliably distinguish the presented categories across all three presentation methods was the lingual gyrus, on the medial surface of the occipital lobe. This area comprises part of the extra-striate visual cortex (V2-V4) and our finding is consistent with the role of these regions in lower-level processing of visual objects (Grill-Spector and Malach, 2004).

Our CFS results are inconsistent with previous findings that category-level information about stimuli suppressed with CFS is available within the ventral temporal cortex (Sterzer et al., 2008, 2009), and with other results linking the presence of tool-related categorical information within the posterior parietal cortex during CFS (Fang and He, 2005). We found that categorical information in the CFS condition was available in much earlier visual regions, all exclusively occipital. This specific result is consistent with a recent study that showed that information is restricted to occipital cortex under CFS and does not extend to either higher-level regions along the ventral and dorsal streams (Hesselmann and Malach, 2011). We found no evidence of categorical information being represented in the superior parietal cortex during CFS. Furthermore, the categorical signal in this region was significantly stronger during visible trials compared to CFS trials. One possibility is that our classifier relied on differences between the categories that were not strictly semantic or categorical, but based on lower-level visual features. However, we attempted to mitigate these kinds of effects by using training and test datasets that contained distinct sets of exemplars from the same category. We also used line drawing images that were not as detailed as those used in the studies mentioned above, which may explain the inconsistencies between our and their results.

The results of the CFF within-method classification were quite different from what was found with the CFS data, and contradict the hypothesis that categorical information about the stimuli was restricted to early visual areas. Information about CFF categories could be recovered both in the fusiform gyrus, a region in temporal cortex that has been consistently implicated in higher-level, categorical processing of visual objects, especially faces (Kanwisher et al., 1997), and in the superior part of the

Table 2 | Names and t-values for all ROIs where at least one of the between-method classifications was significant.

	Full ROI name	CFS->CFF mean d′	CFS->CFF *t*-value	CFF->CFS mean d′	CFF->CFS *t*-value	Size cm^2
SOG	Inferior occipital gyrus and sulcus	0.22	3.39*	0.19	2.24*	23.96
LG	Lingual gyrus	0.04	0.39	0.13	2.19*	42.04
OP	Occipital pole	0.27	2.58*	0.22	3.33*	38.05
CTPS	Posterior transverse collateral sulcus	0.35	3.20*	0.25	2.90*	8.36
MLOS	Middle occipital and lunate sulci	0.22	2.21*	0.12	1.38	17.84

	Full ROI name	VIS->CFS mean d′	VIS->CFS *t*-value	VIS->CFF mean d′	VIS->CFF *t*-value	Size cm^2
IOGS	Inferior occipital gyrus and sulcus	0.28	3.64*	0.50	4.06*	23.96
MOG	Middle occipital gyrus	0.23	3.06*	−0.03	−0.31	33.69
FG	Fusiform gyrus	0.28	3.82*	0.38	5.24*	27.08
LG	Lingual gyrus	0.25	3.06*	−0.06	−0.48	42.04
OP	Occipital pole	0.24	2.57*	0.12	1.32	38.05
CTPS	Posterior transverse collateral sulcus	0.50	3.84*	0.32	2.05*	8.36
MLOS	Middle occipital and lunate sulci	0.17	2.28*	0.32	2.47*	17.84
AOS	Anterior occipital sulcus	0.33	2.67*	−0.18	−1.79	13.24
LOTS	Lateral occipitotemporal sulcus	0.27	2.52*	0.49	3.47*	17.66

**Indicates FDR-corrected $p < 0.05$.*

precentral sulcus of the frontal lobe, which has been implicated in attentional control over visual stimuli (Thompson et al., 2005). A previous fMRI study of CFF compared neural responses to the same stimuli when perceived to be flickering vs. fused, and found that frontal and parietal areas show greater activity to stimuli that appeared to be flickering (Carmel et al., 2006). Others have found that several regions in visual cortex can distinguish fused chromatic flicker from a matched non-flickering control, even when observers cannot (Jiang et al., 2007). In our experiment, we took a slightly different approach by presenting faces and tools that flickered in the same manner, and were seen as fused (and thus invisible) on nearly every trial. This allowed us to ask what areas carried information about the flickering stimuli, rather than the presence or absence of flicker *per se*. This approach has been more commonly used with CFS, where studies have found evidence of category information in ventral temporal and posterior parietal areas (Fang and He, 2005; Sterzer et al., 2008).

We found that several areas outside visual cortex could distinguish between the categories when they were visible, with one of these regions in frontal cortex capable of distinguishing between them during CFF. What stimulus information could be driving classification during each of these presentation methods? Several possibilities exist. The face and tool image sets were identical across visible and both invisible conditions. Moreover, the spatial extent and average luminance of the images was constant between categories, and the exemplars used for classifier training and testing were distinct. Our results are consistent with the possibility that classification is driven by category-level differences, although there remains the possibility of lower-level confounds because of stimulus-level differences. These could be shape-level category differences (e.g., tools were oblong and vertical, whereas faces were rounder, although also vertical) or semantic-level category differences. Shape-level category differences could cause differential activation in areas that process shape or in any region where clear visual topographic maps are known to exist, including in the occipital lobes, posterior parietal lobes, and in the frontal and supplementary eye fields (FEF/SEF) (Hagler and Sereno, 2006; Kastner et al., 2007; Wandell et al., 2007).

Cross-method category classification between the two invisible presentation methods was restricted to ROIs located in posterior occipital cortex, with no other ROIs showing above-chance classification regardless of which method was used as the training/test stimulus. This suggests that only in retinotopically organized areas encoding low-level visual features such as contour boundaries or overall image extent did the CFS and CFF presentations give rise to similar neural representations. Cross-method classification between visible and invisible presentation methods was possible in both occipital and ventral temporal cortex, but this effect only reached significance when the classifier was trained on visible trials and tested on invisible trials. When training on invisible trials and testing on visible trials there was no above-chance classification anywhere. This imbalance may arise because only the more robust stimulus signal available during visible trials is sufficient for training the pattern classifier. Even so, this result suggests that information about both the visual features and the category-relationship of the stimuli are represented in comparable ways between visual and invisible stimuli. Taken together, the cross-method classification analyses reveal an interesting distinction: The two invisible presentation methods only lead to shared representations in regions relatively early in the visual processing stream (lingual gyrus, middle occipital gyrus, middle and lunate occipital sulci), that code information about visual features. On the other hand, each invisible presentation method shares representations with visible presentations in both early visual and later areas that support more category-oriented encoding. This suggests that at least some degree of category information is attained within each invisible presentation method, but that there is a divergence in how category-level information is represented between the two methods after the shared early representation of visual features.

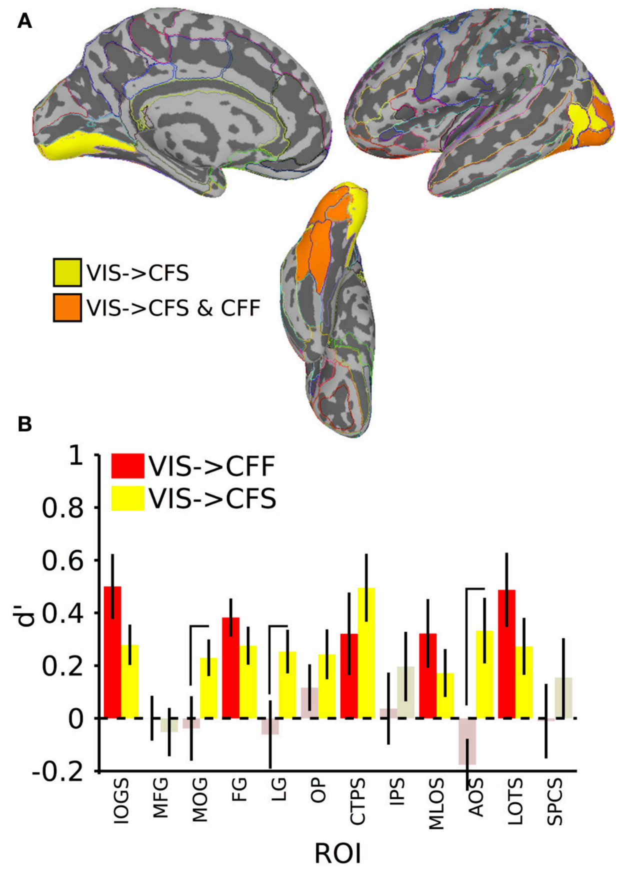


FIGURE 4 | Results for classification from visible to invisible presentation methods. (A) Colored anatomical ROIs indicate regions where category classification was significantly above-chance ($p < 0.05$ FDR-corrected) when performing cross-method category classification from visible to either invisible presentation methods. **(B)** Bar graphs of all regions where significant cross-method category classification was possible. Full region names for the ROI abbreviations are found in **Table 2**. Saturated (yellow and red) colors indicate significant classification, whereas desaturated (light red, light green) colors indicate non-significant classification.

In conclusion, we show that the method used to render a given stimulus invisible has a significant effect on the way in which information about that stimulus can be recovered from neural activity within the human brain. The only region that allowed the recovery of information about object category using all three methods was the lingual gyrus, an area relatively early in the visual processing hierarchy. After this level there appears to be a divergence in bottom-up processing depending on the method used to attain invisibility. In the case of CFS, category information presumably propagates to the lateral occipital surface, and in the case of CFF, information presumably propagates into ventral temporal cortex and to the FEF.

Of the many "C areas" that permitted category decoding under conditions of conscious visibility, different subsets of "U areas" also permitted category decoding under various conditions of unconsciousness or invisibility (whether CFF→CFF, CFS→CFS, CFS→CFF or CFF→CFS). Removing these U areas from the former set of C areas leaves the following subset: anterior occipital sulcus, lateral occipitotemporal sulcus, intraparietal sulcus, and the middle frontal gyrus. It might be tempting to conclude that these "C-U" areas are necessary for conscious vision, and that U areas are not sufficient for conscious vision. However, we simply do not know what it is about neural processing in these areas that makes it possible to classify the category of visible objects, but not invisible objects. We also cannot rule out the possibility that some U areas play a necessary or even sufficient role for consciousness under visible conditions, arising from different forms of neural activity than those that allowed classification under conditions of invisibility in our experiment.

These results have implications for research into the limits of processing in the absence of awareness. They suggest that unconscious processing is not a single, unified phenomenon. Rather, where and how unconscious processing occurs is to a large extent dependent not only on the stimulus being presented, but also on the methodology used to present it. Caution is therefore needed before making strong claims about the nature of conscious or unconscious processing using only a single method for rendering stimuli invisible. Conversely, this should allow future researchers to tailor their stimuli for rendering stimuli invisible in a manner that attains the kinds of unconscious processing they wish to investigate.

REFERENCES

Almeida, J., Mahon, B. Z., Nakayama, K., and Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proc. Natl. Acad. Sci. U.S.A.* 105, 15214–15218. doi: 10.1073/pnas.0805867105

Bahrami, B., Vetter, P., Spolare, E., Pagano, S., Butterworth, B., and Rees, G. (2010). Unconscious numerical priming despite interocular suppression. *Psychol. Sci.* 21, 224–233. doi: 10.1177/0956797609360664

Blake, R. (2001). A primer on binocular rivalry, including current controversies. *Brain Mind* 2, 5–38. doi: 10.1023/A:1017925416289

Blake, R., Fox, R., and McIntyre, C. (1971). Stochastic properties of stabilized-image binocular rivalry alternations. *J. Exp. Psychol.* 88, 327–332. doi: 10.1037/h0030877

Carmel, D., Lavie, N., and Rees, G. (2006). Conscious awareness of flicker in humans involves frontal and parietal cortex. *Curr. Biol.* 16, 907–911. doi: 10.1016/j.cub.2006.03.055

Chao, L. L., Haxby, J. V., and Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat. Neurosci.* 2, 913–919. doi: 10.1038/13217

Cox, D. D., and Savoy, R. L. (2003). Functional magnetic resonance imaging (fMRI) "brain reading": detecting and classifying distributed patterns of fMRI activity in human visual cortex. *Neuroimage* 19, 261–270. doi: 10.1016/S1053-8119(03)00049-1

Destrieux, C., Fischl, B., Dale, A., and Halgren, E. (2010). Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. *Neuroimage* 53, 1–15. doi: 10.1016/j.neuroimage.2010.06.010

Faivre, N., Berthet, V., and Kouider, S. (2012). Nonconscious influences from emotional faces: a comparison of visual crowding, masking, and continuous flash suppression. *Front. Psychol.* 3:129. doi: 10.3389/fpsyg.2012.00129

Fang, F., and He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nat. Neurosci.* 8, 1380–1385. doi: 10.1038/nn1537

Grill-Spector, K., and Malach, R. (2004). The human visual cortex. *Annu. Rev. Neurosci.* 27, 649–677. doi: 10.1146/annurev.neuro.27.070203.144220

Hagler, D. J., and Sereno, M. I. (2006). Spatial maps in frontal and prefrontal cortex. *Neuroimage* 29, 567–577. doi: 10.1016/j.neuroimage.2005.08.058

Hanke, M., Halchenko, Y. O., Sederberg, P. B., Hanson, S. J., Haxby, J. V., and Pollmann, S. (2009). PyMVPA: A python toolbox for multivariate pattern analysis of fMRI data. *Neuroinformatics* 7, 37–53. doi: 10.1007/s12021-008-9041-y

Haxby, J. V., Hoffman, E., and Gobbini, I. (2000). The distributed human neural system for face perception. *Trends Cogn. Sci.* 4, 223–233. doi: 10.1016/S1364-6613(00)01482-0

Hecht, S., and Verrijp, C. D. (1933). The influence of intensity, color and retinal location on the fusion frequency of intermittent illumination. *Proc. Natl. Acad. Sci. U.S.A.* 19, 522–535. doi: 10.1073/pnas.19.5.522

Hesselmann, G., and Malach, R. (2011). The link between fMRI-BOLD activation and perceptual awareness is "stream-invariant" in the human visual system. *Cereb. Cortex* 21, 2829–2837. doi: 10.1093/cercor/bhr085

Hoshiyama, M., Kakigi, R., Takeshima, Y., Miki, K., and Watanabe, S. (2006). Priority of face perception during subliminal stimulation using a new color-opponent flicker stimulation. *Neurosci. Lett.* 402, 57–61. doi: 10.1016/j.neulet.2006.03.054

Ives, H. E. (1911). On heterochromatic photometry. *Philos. Magaz.* 24, 845–853. doi: 10.1080/14786441208634878

Jenkinson, M., Beckmann, C. F., Behrens, T. E., Woolrich, M. W., and Smith, S. M. (2011). FSL. *Neuroimage* 62, 782–790. doi: 10.1016/j.neuroimage.2011.09.015

Jiang, Y., and He, S. (2006). Cortical responses to invisible faces: dissociating subsystems for facial-information processing. *Curr. Biol.* 16, 2023–2029. doi: 10.1016/j.cub.2006.08.084

Jiang, Y., Zhou, K., and He, S. (2007). Human visual cortex responds to invisible chromatic flicker. *Nat. Neurosci.* 10, 657–662. doi: 10.1038/nn1879

Kanwisher, N., McDermott, J., and Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311.

Kastner, S., DeSimone, K., Konen, C. S., Szczepanski, S. M., Weiner, K. S., and Schneider, K. A. (2007). Topographic maps in human frontal cortex revealed in memory-guided saccade and spatial working-memory tasks. *J. Neurophysiol.* 97, 3494–3507. doi: 10.1152/jn.00010.2007

Koch, C., and Tsuchiya, N. (2007). Attention and consciousness: two distinct brain processes. *Trends Cogn. Sci.* 11, 16–22. doi: 10.1016/j.tics.2006.10.012

Lee, B. B., Martin, P. R., and Valberg, A. (1988). The physiological basis of heterochromatic flicker photometry demonstrated in the ganglion cells of the macaque retina. *J. Physiol.* 404, 323–347.

Macknik, S. L. (2006). Visual masking approaches to visual awareness. *Prog. Brain Res.* 155, 177–215. doi: 10.1016/S0079-6123(06)55011-3

Macknik, S. L., and Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual system. *Nat. Neurosci.* 1, 144–149. doi: 10.1038/393

Mahon, B. Z., Schwarzbach, J., and Caramazza, A. (2010). The representation of tools in left parietal cortex is independent of visual experience. *Psychol. Sci.* 21, 764–771. doi: 10.1177/0956797610370754

Moutoussis, K., and Zeki, S. (2002). The relationship between cortical activation and perception investigated with invisible stimuli. *Proc. Natl. Acad. Sci. U.S.A.* 99, 9527–9532. doi: 10.1073/pnas.142305699

Peirce, C. S., and Jastrow, J. (1884). On small differences in sensation. *Memoirs Natl. Acad. Sci.* 3, 73–83.

Saad, Z. S., and Reynolds, R. C. (2012). SUMA. *Neuroimage* 62, 768–773. doi: 10.1016/j.neuroimage.2011.09.016

Sakuraba, S., Sakai, S., Yamanaka, M., Yokosawa, K., and Hirayama, K. (2012). Does the human dorsal stream really process a category for tools? *J. Neurosci.* 32, 3949–3953. doi: 10.1523/JNEUROSCI.3973-11.2012

Schurger, A., Pereira, F., Treisman, A., and Cohen, J. D. (2010). Reproducibility distinguishes conscious from nonconscious neural representations. *Science* 327, 97–99. doi: 10.1126/science.1180029

Sterzer, P., Haynes, J. D., and Rees, G. (2008). Fine-scale activity patterns in high-level visual areas encode the category of invisible objects. *J. Vis.* 8, 10.1–10.12. doi: 10.1167/8.15.10

Sterzer, P., Jalkanen, L., and Rees, G. (2009). Electromagnetic responses to invisible face stimuli during binocular suppression. *Neuroimage* 46, 803–808. doi: 10.1016/j.neuroimage.2009.02.046

Thompson, K. G., Biscoe, K. L., and Sato, T. R. (2005). Neuronal basis of covert spatial attention in the frontal eye field. *J. Neurosci.* 25, 9479–9487. doi: 10.1523/JNEUROSCI.0741-05.2005

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nat. Neurosci.* 8, 1096–1101. doi: 10.1038/nn1500

Vingerhoets, G., Acke, F., Vandemaele, P., and Achten, E. (2009). Tool responsive regions in the posterior parietal cortex: effect of differences in motor goal and target object during imagined transitive movements. *Neuroimage* 47, 1832–1843. doi: 10.1016/j.neuroimage.2009.05.100

Wandell, B. A., Dumoulin, S. O., and Brewer, A. A. (2007). Visual field maps in human cortex. *Neuron* 56, 366–383. doi: 10.1016/j.neuron.2007.10.012

Weiskrantz, L. (1990). *Blindsight: a Case Study and its Implications*. Oxford: Oxford University Press. doi: 10.1093/acprof:oso/9780198521921.001.0001

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 08 March 2014; paper pending published: 01 April 2014; accepted: 28 May 2014; published online: 16 June 2014.

Citation: Fogelson SV, Kohler PJ, Miller KJ, Granger R and Tse PU (2014) Unconscious neural processing differs with method used to render stimuli invisible. Front. Psychol. ***5****:601. doi: 10.3389/fpsyg.2014.00601*

This article was submitted to Consciousness Research, a section of the journal Frontiers in Psychology.