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Weighing the evidence for a dorsal processing bias under continuous flash suppression ☆

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ABSTRACT

With the introduction of continuous flash suppression (CFS) as a method to render stimuli invisible and study unconscious visual processing, a novel hypothesis has gained popularity. It states that processes typically ascribed to the dorsal visual stream can escape CFS and remain functional, while ventral stream processes are suppressed when stimuli are invisible under CFS. This notion of a CFS-specific "dorsal processing bias" has been argued to be in line with core characteristics of the influential dual-stream hypothesis of visual processing which proposes a dissociation between dorsally mediated vision-for-action and ventrally mediated vision-for-perception. Here, we provide an overview of neuroimaging and behavioral studies that either examine this dorsal processing bias or base their conclusions on it. We show that both evidence for preserved ventral processing as well as lack of dorsal processing can be found in studies using CFS. To reconcile the diverging results, differences in the paradigms and their effects are worthy of future research. We conclude that given the current level of information a dorsal processing bias under CFS cannot be universally assumed.

1. Continuous flash suppression

A few years ago, a new method to render stimuli invisible and study unconscious processing has been introduced: continuous flash suppression (CFS) uses high-contrast dynamic images (masks) flashed to one eye, typically at 10 Hz, to suppress a low-contrast stimulus presented to the other eye from visibility (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). Fig. 1 gives an overview over the different types of masks used in a selection of studies that are discussed in this review. One feature that separates CFS from other methods with which images can be rendered invisible – e.g., backward masking – is the duration of possible suppression, which can last up to several seconds (Kim & Blake, 2005; Tsuchiya & Koch, 2005). Its advantage over binocular rivalry on which it is based is that the perceptual dominance does not vary almost unpredictably between the inputs to the two eyes but remains largely with the flickering masks. Whether it is based on the same mechanisms as binocular rivalry or is systematically different remains a subject of debate (Shimaoka & Kaneko, 2011; Tsuchiya et al., 2006).

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CFS has been widely used to investigate unconscious processing, as the extended periods of suppression make it possible to use it on a range of stimuli that could previously not be rendered invisible.

1.1. Degree of processing under CFS

So far the evidence regarding the degree of unconscious processing that occurs during CFS has been mixed (Breitmeyer, 2014; Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014; Yang, Brascamp, Kang, & Blake, 2014).

Using functional magnetic resonance imaging (fMRI), Watanabe et al. (2011) and Yuval-Greenberg and Heeger (2013) investigated neural activity in early visual cortex (V1) under CFS. While the former find similar early visual activation levels for suppressed (invisible) and unsuppressed grating stimuli, the latter find a significant reduction in V1 activity when the grating was rendered invisible.

While responses under CFS are undoubtedly attenuated as shown by adaptation studies (Maruya, Watanabe, & Watanabe, 2008; Tsuchiya & Koch, 2005), the claim that early visual processes are completely abolished under interocular suppression would mean that all responses in higher visual areas to suppressed stimuli would be mediated by subcortical pathways or rely on residual visibility. A framework that has been postulated for binocular rivalry and might also apply to continuous flash suppression supposes that rivalry occurs at multiple levels of the visual hierarchy and not only between the two eyes (Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006).

2. Theoretical implications for dorsal processing under CFS

2.1. The role of dorsal processing according to the dual-stream theory

The dual-stream theory by Milner and Goodale (1995, 2006) proposes the existence of two largely separate visual systems, the ventral visual system, or ventral stream, which is associated with consciously accessible 'vision-for-perception' and the dorsal visual system, or dorsal stream, which mediates consciously inaccessible 'vision-for-action'. This theory has sparked widespread empirical examination of its claims and remains one of the most influential models of visual processing in the primate brain.

According to the theory, the dorsal stream's main task is the real-time visual guidance of actions or their preparation, transiently coding the targets of these actions in egocentric coordinates (Schenk & Mcintosh, 2010). Most importantly, its computations operate independently of visual awareness, meaning that they are neither available for conscious awareness, nor evoking it (Milner, 2012; Schenk & Mcintosh, 2010).

Traditionally this latter point has been demonstrated in patients with relatively stream-specific lesions. Patient D.F., for example, whose extensive bilateral ventral stream damage resulted in visual form agnosia, is capable of grasping for objects while being unable to judge or describe the perceptual components of the same objects. Her remaining visual capacities are attributed to dorsal stream processing (Milner & Goodale, 2008).

In neurologically healthy participants, so far the most prominent demonstration of dorsal stream computations stems from studies using visual illusions. Aglioti, DeSouza, and Goodale (1995) reported that grasping (taken as a measure for dorsal processing) may be immune to the Ebbinghaus size illusion while perceptual measures were not. Other studies, however, do not support this dissociation (e.g., Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; for reviews see: Franz & Gegenfurtner, 2008; Westwood & Goodale, 2011).

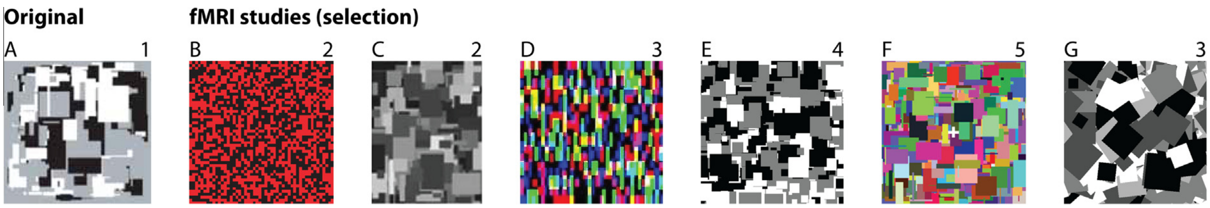

Fig. 1. The different CFS masks used in the original CFS study and some of the discussed fMRI studies. Masks range from noise pixels to Mondrian- or other patterns: (A) Tsuchiya and Koch (2005), reprinted by permission from Macmillan Publishers Ltd: Nature Neuroscience. From "Continuous flash suppression reduces negative afterimages." by N. Tsuchiya and C. Koch, Nature Neuroscience, 8(8), p. 1097, copyright 2005. (B) Fang and He (2005), reprinted by permission from Macmillan Publishers Ltd: Nature Neuroscience. From "Cortical responses to invisible objects in the human dorsal and ventral pathways." by F. Fang and S. He, Nature Neuroscience, 10, p. 1381, copyright 2005. (C) Jiang and He (2006), reprinted from Current Biology, 16, Jiang, Y., & He, S., "Cortical responses to invisible faces: Dissociating subsystems for facial-information processing.", p. 2024, copyright 2006, with permission from Elsevier. (D) Sterzer et al. (2008), image provided by the authors, (E) Hesselmann and Malach (2011), image provided by the authors, (F) Fogelson et al. (2014), reprinted from "Unconscious neural processing differs with method used to render stimuli invisible." by S. V. Fogelson, P. J. Kohler, K. J. Miller, R. Granger, & P. U. Tse, 2014, Frontiers in Psychology, 5, 601, p. 4, copyright 2014. (G) Ludwig et al. (2015), image provided by the authors. Different presentation techniques are used to achieve dichoptic stimulation: (1) mirror stereoscope, (2) anaglyph glasses*, (3) cardboard divider (+prism glasses), (4) linear polarizing filters*, (5) digital binocular presentation goggles. In the presentation techniques marked with '*', crosstalk is possible. Crosstalk occurs when stimulus information that is meant to reach only one of the eyes also reaches the other eye, albeit usually in a very degraded form.