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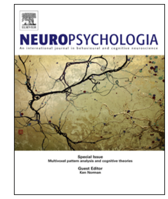

Learning to detect but not to grasp suppressed visual stimuli

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ABSTRACT

A central implication of the two-visual-systems hypothesis (TVSH) is that the dorsal visuomotor system (vision-for-action) can make use of invisible information, whereas the ventral system (vision-for-perception) cannot (Milner & Goodale, 1995). Therefore, actions such as grasping movements should be influenced by invisible information while conscious reports remain unaffected. To test this assumption, we used a dichoptic stimulation technique – continuous flash suppression (CFS) – which has the potency to render stimuli invisible for up to seconds (Tsuchiya & Koch, 2005). In two experiments using CFS, participants were asked to grasp for invisible bars of different sizes (Experiment 1) or orientations (Experiment 2), or to report both measures verbally. Target visibility was measured trial-by-trial using the perceptual awareness scale (PAS). We found no evidence for the use of invisible information by the visuomotor system despite extensive training (600 trials) and the availability of haptic feedback. Participants neither learned to scale their maximum grip aperture to the size of the invisible stimulus, nor to align their hand to its orientation. Careful control of stimulus visibility across training sessions, however, revealed a robust tendency towards decreasing perceptual thresholds under CFS. We discuss our results within the framework of the TVSH and with respect to alternative models which emphasize the close functional interaction between the dorsal and ventral visual systems.

1. Introduction

The 'two visual systems' hypothesis (TVSH) proposed by Milner and Goodale (1995) remains one of the most influential models of visual processing in the primate brain. It assumes a dissociation between consciously accessible 'vision-for-perception', mediated by the ventral cortical pathway, and consciously inaccessible 'vision-for-action', mediated by the dorsal pathway (Milner, 2012). One of the primary pillars this model rests on are the studies performed on patient D.F., who suffers from visual form agnosia as a result of extensive bilateral ventral stream damage following carbon monoxide poisoning (James, Culham, Humphrey, Milner, & Goodale, 2003; Milner et al. 1991; also see: Karnath, Rueter, Mandler, & Himmelbach, 2009). D.F. can successfully grasp for objects while she is unable to perform perceptual judgements such as size or shape estimation on them and her remaining visual capacities have been attributed to dorsal stream processes (Culham et al., 2003; Milner & Goodale, 2008).

In neurologically healthy participants, the demonstration of perception-action dissociations has proven to be difficult. A first study that showed that grasping (taken as a measure for dorsal processing) may be immune to the Ebbinghaus size illusion while perceptual measures were not (Aglioti, DeSouza, & Goodale, 1995) has prompted a multitude of studies, many of which do not support a dissociation (e.g., Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; for reviews see Franz & Gegenfurtner, 2008; and Westwood & Goodale, 2011). Another way to probe this dissociation in healthy participants has been paved by the introduction of a new technique called continuous flash suppression (CFS) which can render stimuli invisible for up to several seconds by flashing high-contrast images to one eye while showing the target stimulus to the other eye (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006).

Evidence from behavioral priming experiments (Almeida, Mahon, Nakayama, & Caramazza, 2008; Sakuraba, Sakai, Yamanaka, Yokosawa, & Hirayama, 2012) and neuroimaging studies (Sterzer, Haynes, & Rees, 2008; Troiani, Price, & Schultz, 2012) shows that stimulus information suppressed from awareness with CFS can reach higher-order visual areas and influence behavior.

It has been suggested that CFS could be used to "isolate" dorsal visual processing, i.e., to leave nonconscious visuomotor processes

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mediated by the dorsal stream intact while disrupting conscious perception mediated by the ventral stream (Fang & He, 2005; Lin & He, 2009; but see: Hesselmann & Malach, 2011; Hesselmann, 2013). If this was the case, one could expect participants to show above chance performance in grasping invisible stimuli, while not being able to report the stimuli's features verbally. Such behavior would classify as a form of "blindsight", a rare dissociation in patients with lesions to primary visual cortex (V1), typically defined as residual forced-choice visual function in the absence of subjective awareness (Cowey, 2004; Stoerig & Cowey, 2007). According to the taxonomy for different blindsight subtypes proposed by Danckert & Rossetti, accurately acting upon blind field stimuli based on preserved activity in the dorsal stream classifies as "action-blindsight" (Danckert & Rossetti, 2005). We reasoned that testing for a similar perception-action dissociation in healthy observers using CFS would constitute a critical test for the TVSH, in particular its claim that ventral stream processes are associated with visual awareness, while dorsal processes are not. In this study, we aimed to generate a blindsight-like situation in normal observers to test whether information unavailable to conscious report would still be processed in a way to enable grasping for objects of different sizes (Experiment 1) or orientations (Experiment 2).

2. Material and methods

2.1. Participants

All participants had normal or corrected-to-normal vision, were naïve to the purpose of the study, and were either paid for participation or received course credit. Procedures conformed to local ethics guidelines and all observers gave informed written consent. Five participants (two female) took part in Experiment 1. Their mean age was 23.8 years (range 19–30). They scored on average 86.82 (range 66.67–100) on the Edinburgh Handedness Inventory and were thus all right-handed. Two further participants were invited but as the CFS-method did not work on them (contrast sensitivity thresholds in the non-dominant eye were only marginally increased by CFS-masks to the dominant eye), they did not take part in the main experiment. Six participants (five female) completed Experiment 2. Their mean age was 26.5 years (range 20–29). They scored on average 75.42 (range 54.55–90.48) on the Edinburgh Handedness Inventory and were thus all right-handed.

2.2. Apparatus and setup

Participants carried out the grasping movements with the right hand below a stimulation mirror, where real objects were placed to be picked up by the participants for veridical haptic feedback (Fig. 1). The observers were seated in an environment with dim background lighting and viewed the dichoptic images on a 22″ screen (Samsung SyncMaster 2233RZ; effective screen diagonal: 55.8 cm) with a spatial resolution of 1680 × 1050 pixels, via a mirror setup (Fig. 1) through prism glasses. Together with these glasses, a cardboard divider that was installed between screen and mirror prevented any crosstalk (Schurger, 2009). To stabilize head position the participants placed their heads on a chinrest and looked down into the mirror through which they saw the stimuli drawn on the screen above. Care was taken that all virtual stimuli (from now on "rectangles") were perceived at the same position in space as the real objects that the participants had to grasp (from now on "cuboids").

Visual stimuli were generated with Matlab 7.9.0 (MathWorks Inc., Natick, MA) and the Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997) and displayed via an IBM-compatible computer with an NVIDIA Quadro FX4600 graphics card. The viewing distance from the eyes to the screen (including distances within the mirror system) was 50 cm, resulting in each pixel subtending approximately 0.039° of visual angle. The background luminance was 30.3 cd/m². The trajectories of the finger movements were recorded by an Optotrak Certus system (Northern Digital Inc., Waterloo, Ontario, Canada) at a sampling rate of 200 Hz. An infrared light-emitting diode (IRED) was attached to the nails of both thumb and index finger of the right hand using adhesive pastels (UHU-patafix, UHU GmbH, Bühl, Germany).

2.3. Stimuli

In Experiment 1, participants grasped objects of five different sizes or verbally reported their size. Five cuboids made of gray plastic served as target objects. The bottom side of each cuboid was laminated with felt to attenuate any noises caused by handling of the cuboid. The objects differed in the dimension of length (2, 3, 4, 5, and 6 cm) but were of a constant width and height (1.5 cm). All objects were grasped along their length. Their weight was 6, 9, 12, 16, and 19 g. On each trial objects were placed at the same position marked with a pin upon which the object was affixed.

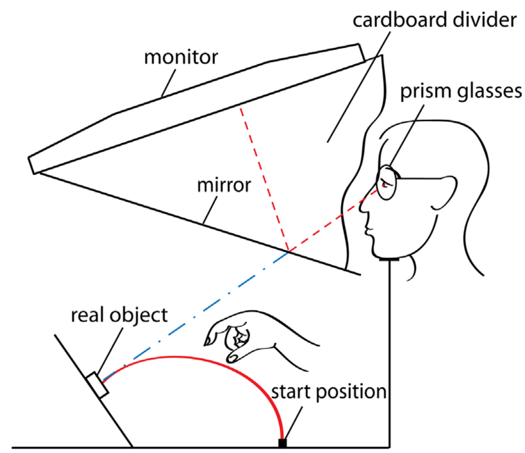

Fig. 1. Experimental setup in Experiments 1 and 2. Participants saw a virtual object that was displayed on the monitor reflected in the mirror (indicated by dashed red line). A calibration procedure made sure that the virtual object was seen at the same position as the corresponding real object. Participants did not see the real object or their hand, the dotted blue line indicates only a theoretical line-of-sight. On each grasping trial, participants performed a grasping movement (solid red line) toward the real object which started at a fixed position and ended with touching the real object. For dichoptic stimulation, a cardboard divider was installed between the screen and the mirror, and participants wore prism glasses to aid binocular fusion. To render virtual objects invisible, high contrast Mondrian images were flashed at 10 Hz to the dominant eye, while the virtual object was presented to the other eye. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

In Experiment 2, participants were asked to grasp objects of two different orientations (0° and 90°) or to report their orientation verbally. One cuboid (2 × 4 × 1.5 cm, 16 g) was grasped along its length, which was sometimes horizontally and sometimes vertically aligned.

The stimuli shown on the screen were rectangular 2D outlines of the 3D cuboids which measured from 2.75° to 8.49° of visual angle in length and 2.06° in width (Experiment 1), or 5.45° in length and 3.97° in width (Experiment 2), respectively. Their lines were 0.08° thick and the stimuli were presented at fixation.

The luminance of the to-be-grasped edges was determined in a staircase procedure that preceded the experiments (see Procedure) and decreased after a series of trials in which the participant reported visibility of the stimulus to maintain full invisibility. The luminance of the other edges was set to a constant 26.72 cd/m².

2.4. Interocular masking

We used an interocular suppression paradigm (Tsuchiya & Koch, 2005) called continuous flash suppression (CFS). This technique uses high-contrast dynamic images flashed to one eye to suppress images presented to the other eye from awareness. The images consisted of rectangles of eight different colors (white, black, red, green, blue, yellow, pink and cyan, 0.2–170 cd/m²) and sizes ranging from 1.5% to 5.7% of the size of the CFS area, which measured 16.97°. The rectangles were positioned at random locations on the mask image. 25 of these images were produced and flashed in random order at 10 Hz to the dominant eye. This rendered the stimulus presented to the non-dominant eye largely invisible. To promote stable binocular fusion during dichoptic presentation, a square frame was presented around the fixation point. Its outer and inner dimensions were 18.07° and 16.97° of visual angle, respectively. The frame consisted of random noise pixels.

It is important to note that although it has been shown that the kinematics of prehension are altered under monocular viewing conditions, monocular vision does support reliable and accurate grasping movements in normal observers (Loftus, Servos, Goodale, Mendarozqueta, & Mon-Williams, 2004; Verhagen, Dijkerman, Grol, & Toni, 2008).

In patients with visual form agnosia, the removal of binocular cues has been shown to disrupt the calibration of grasping, but patient D.F. showed preserved grip size scaling in an analysis where the distance of the to-be-grasped object was disregarded (Marotta, Behrmann, & Goodale, 1997). This finding suggests that binocular cues are important for grasping only when different target distances play a role. In our study, however, the objects were always placed at the same position.