

Visuomotor system uses target features unavailable to conscious awareness

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After lesions to primary visual cortex, patients lack conscious awareness of visual stimuli. Interestingly, however, some retain the ability to make accurate judgments about the visual world (i.e., so-called blindsight). Similarly, damage to inferior occipitotemporal regions of cortex (e.g., lateral occipital cortex) can result in an inability to perceive object properties while retaining the ability to act on them (i.e., visual form agnosia). In the present work, we demonstrate that the ability to interact with objects in the absence of conscious awareness is not isolated to those with restricted neuropathologic conditions. Specifically, neurologically intact individuals are able to program and execute goal-directed reaching movements to a target object without awareness of extrinsic target properties; they accurately tune the dynamics of their movement and modulate it online without conscious access to features of the goal object. Thus, the planning and execution of actions are not dependent on conscious awareness of the environment, suggesting that the phenomenon of blindsight (and agnosia) reflect normal conditions of the visual system.

action | agnosia | blindsight | consciousness | perception

One of the key roles of vision is to direct movements aimed at objects. The consequent subjective experience of movement production is that we have conscious control over the visual information that we use to execute action. However, individuals who have lesions to primary visual cortex (V1) lack conscious awareness of visual stimuli while retaining limited ability to make accurate judgments about the visual world (i.e., so-called “blindsight”) (1). In the present work, we demonstrate that neurologically intact individuals are able to program and execute goal-directed reaching movements without explicit awareness of extrinsic target properties (e.g., size). Thus, the planning and execution of actions may be completed without the conscious awareness of metrical environmental properties. These results suggest that blindsight is a normal condition of the visual system rather than a neuropathologic condition arising from damage to cortex.

Perhaps the most widely studied blindsight patient is known as “GY,” who consciously reports that he cannot distinguish stimuli within his blind hemifield (1). Within this same hemifield, GY can generally follow the path of a moving stimulus, verbally identify color stimuli, and accurately point to objects, despite having no conscious percept of these features. However, the deficit exhibited by GY is profound, spanning perceptual and sensory aspects of the visual system, and does not occur universally after damage to V1. Thus, it is unclear whether the preserved abilities of GY reflect a fundamental property of the visual system or whether these residual visuomotor functions are artifacts of his significant injuries.

Patient DF (2) exemplifies a more subtle demonstration of the independence of consciousness and visual perception. After damage to regions of the ventrolateral occipitotemporal cortex [e.g., lateral occipital cortex (LOC)] (3), DF exhibits an inability to recognize objects (i.e., visual form agnosia). DF cannot identify simple line drawings of familiar objects nor can she

determine their size or orientation. However, when asked to pick up an object, she does so quickly (although slower than age-matched controls) and accurately, without hesitation; that is, her movements are metrically tuned to the size and orientation of the object.

Based on the clinical observations of GY and DF, we investigated the conscious access to visual object size information to support the control of goal-directed reaching movements in neurologically intact individuals. Participants pointed to targets by using a masking paradigm developed by Di Lollo *et al.* (4) whereby conscious perception of the object is removed by means of an object substitution-masking paradigm (see Fig. 1). If the preserved visuomotor functions of GY and DF (in the absence of visual object awareness) reflect normative features of the visual system, we predicted that participants would be able to accurately reach to targets regardless of whether the target was consciously perceived or not; participants should demonstrate a speed–accuracy tradeoff. Specifically, participant movement times should conform to Fitts’ Law (5). In this information-derived account of action, the accuracy of movements and the speed with they are executed are described by a lawful relation [i.e., $MT = \log_2(2a/w)$, where MT is movement time, a is movement amplitude, and w is target width]; in short, people move more slowly to small targets or targets that are far away. Moreover, a corollary prediction of our normative function hypothesis is that movement kinematics during such reaches should reflect target-derived movement control (e.g., increased time after peak velocity) that is independent of explicit awareness of object size.

Results and Discussion

Initially, to confirm the efficacy of the masking paradigm for removing conscious awareness, participants performed a pure perceptual task; simply, participants were to judge the size (small or large) of the cued target. Overall, participants were better able to make judgments regarding the cued target when conscious awareness was present [$t(9) = 13.70$, $P < 0.001$]. Specifically, when presented with a perceptually masked object (unconscious condition), participants were unable to report the size of the target above chance levels [two size forced choice task: mean correct = 56%, mean $d' = 0.07$, $t(9) = 0.56$, $P > 0.05$]. Conversely, when presented with unmasked choices (i.e., conscious condition), participant performance was highly accurate and significantly improved [mean correct = 94%, mean $d' = 2.24$, $t(9) = 16.8$, $P < 0.001$]. Further, in the unconscious

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Abbreviations: LOC, lateral occipital cortex; V1, primary visual cortex.

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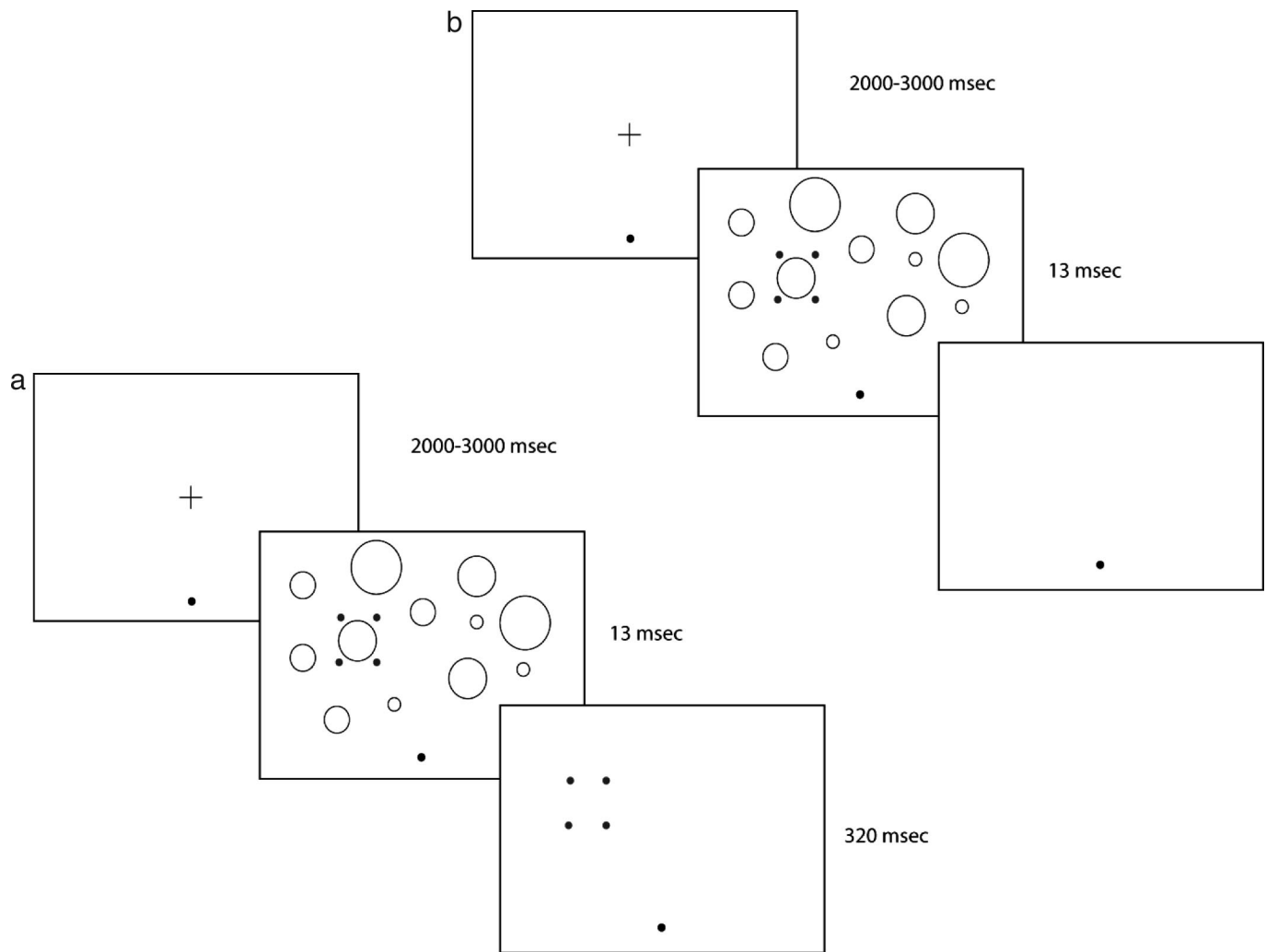


Fig. 1. Display sequence for experiment. Participants initially observed a fixation cross and home position. After a variable foreperiod (1–3 s), an array of circles appeared; one circle was identified as the target by 4 red cue circles. In all cases the participant was asked to point to the middle of the target as quickly and accurately as possible. (a) Unconscious condition. The red cue circles remained present after removal of the array. This results in object substitution masking (4, 14), where participants have no conscious access to target properties (e.g., size). (b) Conscious condition. The red cue circles were removed concurrently with the array. In this condition, participants could consciously report the target properties.

condition, participants spontaneously reported that they were not confident in their estimations and that they were only guessing at target size. Thus, self-report and behavioral data indicate strongly that participants did not consciously perceive the metric properties of the cued target when presented in a masked fashion.

In contrast to the perceptual data, results for the pointing task did not vary between conscious and unconscious target conditions. Specifically, movement time results demonstrated reliable speed/accuracy trade-offs (5) [$F(4, 36) = 9.86, P < 0.01$; see Fig. 2] regardless of level of consciousness (see Table 1); no influence of consciousness was observed [main effect: $F(1, 9) = 1.44$, interaction: $F(4, 36) = 0.78; P > 0.2$]. Participants spent proportionally more time after peak velocity as a function of decreasing target size [$F(4, 36) = 3.11, P < 0.05$]: a result indicative that online regulation of the movement was predicated on the extrinsic target properties. Moreover, as target size decreased, participants adjusted the terminus of their movement accordingly, varying the degree of undershoot error [$F(4, 36) = 3.13, P < 0.05$] in a manner consistent with an energy minimization strategy (6, 7). This type of conservative strategy is

similarly consistent with normal, target-derived, movement planning.

Importantly, these results demonstrate that despite participants' inability to consciously report a metrical target property (i.e., size), their visuomotor control system remained responsive to these cues. This would suggest that the dorsal pathway receives target information during the initial "feedforward" projection from V1, before the recurrent mask, and presumably stores this information transiently for future motor production (8). Further, it is precisely this type of metrical information that the visual form agnostic DF is thought to use when executing effective reaching and grasping responses, despite having no functional ventral stream (2, 3, 9). Thus, our neurologically intact participants are behaving in a fashion consistent with visual form agnosia.

However, unlike DF who can report some properties of objects [e.g., color and texture (3)], participants in our study have no such (limited) conscious awareness. Thus, the behavioral data demonstrated here appear consistent with a special case of blindsight: action blindsight. Danckert and Rosetti (10) suggest that blindsight patients can be subdivided according to residual functions and neural pathways. Those with "attention blind-

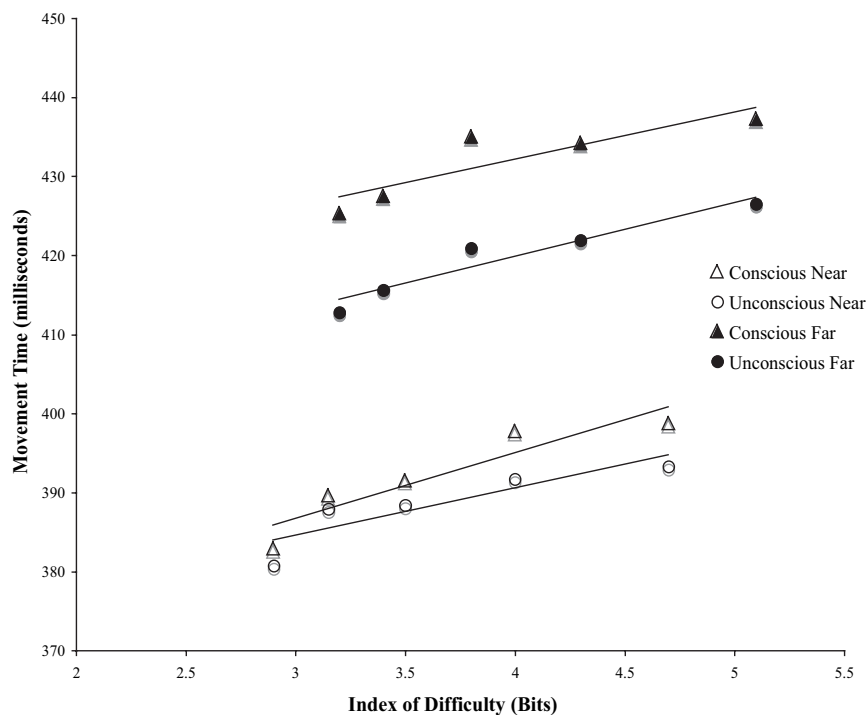


Fig. 2. Depiction of speed-accuracy tradeoff. Regardless of target or consciousness conditions, participants clearly demonstrated movement times dependent on target size. This convincingly demonstrates that movements to unconsciously presented targets are constrained by the same basic principles as those for consciously perceived targets [i.e., Fitts' Law (5)].

sight" retain the ability to orient attention and detect motion, whereas "agnosopsia" permits form discrimination. Finally, and most germane to this discussion, persons with "action blindsight" are availed the use of accurate metrical information for visuomotor localization of stimuli presented within the scotoma. Unlike individuals with visual form agnosia, who have lesions in LOC (3), the preserved visuomotor abilities of action-blindsight patients presumably reflect the integrity of retino-tectal projections terminating in posterior parietal cortices,[†] including inferior (IPL) and superior (SPL) lobules (10–12).

Thus, this experiment provides compelling evidence of action blindsight in neurologically intact adults. Although others have shown intrusions of unconsciously presented information on behaviors such as movement selection (13) and target localization (14–16), a demonstration that intrinsic target features (i.e., size) can influence movement planning and control in the absence of conscious awareness has not been reported previously. Combined with the numerous demonstrations of attention blindsight in neurologically intact adults [e.g., covert orienting (17), inattentional blindness (18)], the following question arises: To what degree does blindsight represent the status quo in the visual system?

Our data, combined with those of others (2, 3, 8, 19, 20), provide a cohesive picture of a visual system that is largely unavailable to and unreliable on conscious awareness. Specifically, Goodale and Milner's (2, 3) perception–action model (PAM) asserts the independence of (conscious) perception and the (unconscious) visual regulation of action. In this model, extrastriate projections to the LOC (i.e., the ventral visual pathway) provide information relevant to the perceptual qualities and identity of an object, whereas projections to the

posterior parietal cortex (i.e., the dorsal visual pathway) provide information relevant to the planning and control of action (3). Consistent with the PAM, we observed that unconsciously presented targets influenced the initiation and execution of goal-directed movement regardless of the participant's explicit awareness.

Thus, we have demonstrated that one can move to things that one cannot consciously see and that one's actions are organized based on features of which one is not aware. It would appear that the percept of awareness is constructed post hoc to enable knowledge accumulation and is not necessary for the planning and execution of action. Further, these data are consistent with the clinical data and suggest that blindsight is a fundamental property of the visual system (1, 10).

Methods

Participants. Ten University of Saskatchewan students (five men and five women) with a mean age of 22.7 years were recruited for this study. All had normal or corrected-to-normal vision. This research was performed in with the approval of the Office of Research Services (Behavioural Research Ethics Board, University of Saskatchewan) and in accord with the Declaration of Helsinki (1964, 2000).

Apparatus. All trials were performed on a rear-projection screen, mounted at waist level and angled at 45° toward the participant.

Table 1. Summary of linear regression findings

State	Amplitude	Equation	R ²
Unconscious	Near	$y = 5.98x + 367$	0.781
	Far	$y = 6.80x + 393$	0.922
Conscious	Near	$y = 8.33x + 361$	0.856
	Far	$y = 5.95x + 408$	0.775

[†]It should be noted that evidence regarding the integrity and utilization of retino-tectal pathways for carriage of visual information to extrastriate regions is based on findings in the macaque and therefore are only speculative with regard to human function.

Targets were projected on the screen via a NEC VT465 LCD projector operating at 1800 ANSI lumens. An infrared emitting diode (IRED) was placed on the fingernail of the right index finger of participants (i.e., the pointing finger). IRED position data were tracked by using a 3D motion analysis system (Visualize VZ3000; Phoenix Technologies, Burnaby, BC, Canada), recording at 200 Hz.

Procedure. At the beginning of all trials, participants placed their pointing finger on a home position and fixated on a centrally presented cross (see Fig. 1). After a random foreperiod (2–3 s), the cross was replaced by an array of 20 circles ranging in size from 1.5 to 5.5 cm in diameter and at distances of 10–35 cm from the home position. A square surround of 4 red cue circles (36 cm² area) indicated the target circle. The target varied in position, although it was always either 20 cm (the short movement) or 25 cm (the long movement) from the home position (radial distance). Further, the red cue circles acted to both identify the target and mask the target [object replacement masking (4, 21)]. The array of circles were projected for 13 ms. Upon removal of the array of circles, the cue circles either remained visible for an additional 320 ms (unconscious condition), or they simultaneously disappeared and were replaced by a blank screen projected for 320 ms (conscious condition).

Participants completed two types of trials: (i) Participants had to point to the target (action trials, $n = 200$); followed by (ii) participants had to judge the size of the target (perception trials, $n = 16$). For the action trials, participants were instructed to point to the target “as quickly and accurately as possible” immediately upon presentation. For each combination of amplitude (2), target size (5), and condition (2), 10 trials were performed. Trials were blocked by condition (conscious, unconscious), with the order counterbalanced between blocks. Com-

binations of target size and amplitude were combined pseudorandomly within each block.

For the perception trials, participants completed a forced-choice binary decision (i.e., “small” or “large”). To avoid confusion with the naming of intermediate-sized targets, only the largest (5.5 cm) and smallest (1.5 cm) target sizes were presented. Target amplitude, location, and condition procedures were otherwise identical to action trials. For each combination of target size (2) and mask (2), 8 trials were presented (chance score = 50%, 8 per condition). Trials were blocked by condition (conscious, unconscious), with the order counterbalanced between blocks. Combinations of target size and amplitude were combined pseudorandomly within each block.

Data Analysis. Three-dimensional kinematic data were collected at 200 Hz for 2 s. Position data were filtered off-line by using a second-order dual-pass (zero-lag) Butterworth filter employing a low-pass cut-off frequency of 15 Hz. Subsequently, instantaneous velocities were calculated by differentiating the displacement data using a three-point central finite difference algorithm. The criterion for movement onset was an index finger velocity that was >50 mm/s for 10 consecutive frames (i.e., 50 ms). Movement offset was determined through a two-step procedure. The first criterion was finger velocity of <50 mm/s. Second, the first sample from within the velocity bandwidth in which no further finger displacement was detected in the anteroposterior axis was marked for movement offset. Movement time (*MT*) was defined as the latency between movement onset (reaction time) and offset.

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