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Perception-action dissociations depend on the luminance contrast of the stimuli

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Deplancke A, Madelain L, Gorea A, Coello Y. Perception-action dissociations depend on the luminance contrast of the stimuli. *J Neurophysiol* 110: 1974–1983, 2013. First published July 24, 2013; doi:10.1152/jn.00575.2012.—The observation that near-threshold low-contrast visual distractors can equally influence perceptual state and goal-directed motor responses was recently taken as an argument against a sharp separation between a conscious vision for perception and an unconscious vision for action. However, data supporting the dual visual system theory have principally involved high-contrast stimuli. In the present study, we assessed the effect of varying the contrast of a near-threshold visual distractor while keeping its visibility constant with backward noise masks. Eight participants performed fast manual reaching movements toward a highly visible target while subsequently reporting the presence/absence of a near-threshold distractor appearing at the opposite location with respect to the body midline. For all distractor contrasts, hand trajectory deviations toward the distractor were observed when the distractor was present and detected. When the distractor remained undetected deviations also occurred, but for higher contrasts. The subliminal motor effect traditionally observed in visual masking studies may therefore primarily depend on the luminance contrast of the interfering stimuli. These results suggest that dissociations between perceptual and motor responses can be explained by a single-signal model involving differential thresholds for perception and action that are specifically modulated as a function of both the requirements of the task and the contrast level of the stimuli. Such modulation is compatible with neurophysiological accounts of visual masking in which feedforward activation to—and feedback activation from—higher visual areas are correlated with the actual presence of the stimulation and its conscious perception, respectively.

perception action; visual masking; visual distractor; hand movements; trajectory deviations

IN THE LAST DECADES, numerous studies have provided converging arguments favoring the existence of a dual visual system based on two anatomically and functionally distinct pathways for perception and action: a ventral stream projecting from the primary visual cortex to the inferior temporal cortex and dedicated to object identification and conscious perception and a dorsal stream in charge of object-directed actions and projecting from the primary visual cortex to the posterior parietal cortex (Goodale 2008; Goodale et al. 2005; Goodale and Milner 1992; Milner and Goodale 1995, 2008). One of the main arguments in favor of this perception-action dichotomy came from the differential effects of illusory visual stimuli on perceptual and motor responses (Aglioti et al. 1995; Bridgeman et al. 1981; Coello et al. 2007; Ganel et al. 2007; Kroliczak et al. 2006; Zivotofsky 2004) as well as from visual masking experiments in which even fully masked, i.e., not consciously perceived, primes or distractors were found to influence reaction times (RTs) and kinematics aspects of reaching movements (Amundson and Bernstein 1973; Binsted et al. 2007; Ogmen et al. 2003; Schmidt 2002; Taylor and McCloskey 1990; Van der Stigchel et al. 2009).

A thorough analysis of these studies, however, highlighted several theoretical and methodological flaws weakening the claim that a clear-cut separation exists between a conscious vision for perception and an unconscious vision for action, as inferred from visual illusion (Bruno et al. 2010; Bruno and Franz 2009; Franz et al. 2001; Franz and Gegenfurtner 2008; Smeets et al. 2002; Smeets and Brenner 1999, 2001, 2006) and visual masking (Holender and Duscherer 2004; Reingold and Merikle 1990; Waszak et al. 2007) studies. The criticisms emphasized the necessity to take into account critical experimental factors, such as the nature of the task, the characteristics of the stimuli, or the difficulty (or even impossibility) of matching the conditions under which motor and perceptual responses were recorded, before drawing general conclusions about a perception-action dissociation within the visual system (Bruno et al. 2010; Cardoso-Leite and Gorea 2010; Smeets and Brenner 2006).

Recent studies have provided new insights into this debate by assessing, on a trial-by-trial basis, both perceptual and motor responses in the presence of near-threshold visual stimuli (Cardoso-Leite et al. 2007, 2009; Deplancke et al. 2010; Waszak and Gorea 2004). In these experiments, participants usually performed a motor task involving a highly visible target (RT, goal-directed reaching movement, or ocular saccade) and subsequently judged the presence/absence of a near-threshold distractor or prime (perceptual task) appearing temporally close to the target onset. The Yes/No design of the perceptual task allows a trial-by-trial classification of the motor responses according to the four standard response categories of signal detection theory (SDT; Green and Swets 1966): Hits (distractor present and detected), Misses (present but not detected), Correct Rejections (absent and not detected), and False Alarms (absent but detected). In contradiction of the widespread idea of a compulsory effect of not consciously perceived visual stimuli on motor responses (Binsted et al. 2007; Goodale 2008; Milner and Goodale 1995, 2008; Ogmen et al. 2003; Schmidt 2002; Taylor and McCloskey 1990), the main outcome of these studies was that perceptual and motor responses (i.e., manual RTs: Cardoso-Leite et al. 2007, 2009; Waszak et al. 2007; Waszak and Gorea 2004; saccade trajectories: Cardoso-Leite and Gorea 2009; or manual trajectories:

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Deplancke et al. 2010) were strongly coupled: on most occasions motor responses were affected by the presence of a distractor or prime only when the latter was consciously perceived (Hit trials).

Trajectory deviations of ocular saccades (for a review, see Van Der Stigchel et al. 2006) or hand reaching movements (Lee 1999; Sailer et al. 2002; Song and Nakayama 2008; Tipper et al. 1997) in the presence of irrelevant distractors have been interpreted as resulting from a competitive influence of these distractors during the process of target selection for action (Tipper et al. 1997, 2000, 2001). According to these authors, each stimulus of a visual scene (i.e., target and distractors) activates a specific region in the retinotopic motor map of the neurophysiological structures involved in visual target selection (e.g., superior colliculus), with the end point location of the reaching response being specified by spatially averaging these activations (McPeek and Keller 2004; Robinson 1972; Wurtz et al. 1980). For short-RT responses (resulting from excitatory processes only), a motor trajectory deviation toward the distractor is typically observed; for longer RTs (i.e., >200 ms), a reactive inhibition of the irrelevant distractor-triggered activity leads to a deviation away from this distractor (McSorley et al. 2006; Tipper et al. 2001; Van der Stigchel and Theeuwes 2005, 2008).

Using near-threshold distractors meant to interfere with target selection during the early stages of visual processing and thus with subsequent reaching trajectories, Deplancke et al. (2010) and Cardoso-Leite and Gorea (2009), respectively, found that deviations toward and away from the distractor were highly correlated with the perceptual state evoked by the distractor, in that they were mainly observed in Hit trials. However, Deplancke et al. (2010) also reported a marginal effect of distractors on RTs in Miss trials when the distractors' contrast was high.[1] This observation suggested the possibility of a different effect of the distractor on perceptual and motor responses depending on the contrast level of the distractor (see Waszak and Gorea 2004 and Waszak et al. 2007 for a similar suggestion in RT experiments). The purpose of the present study was to test this hypothesis by assessing the effect of varying the contrast of a near-threshold distractor on manual motor responses.

In the present experiment, participants performed a dual task: a fast pointing movement toward a highly suprathreshold target appearing randomly at one of two possible locations and a detection task bearing on the presence/absence of a close-to-threshold distractor concurrently presented at the symmetrical location with respect to the target along the sagittal plane. The contrast of the near-threshold distractor was varied across the conditions while keeping its visibility constant through the addition of a backward noise mask. Motor performances were classified according to the participants' perceptual state, i.e., Hits, Misses, False Alarms, and Correct Rejections (used as baseline). To focus on the early stages of visual processing (excitatory processes involved in target selection), we also constrained participants to produce short-RT motor responses (McSorley et al. 2006).

METHODS

Participants

Eight voluntary naive participants were included in this experiment (5 men, 3 women; mean age 27 yr). They all had normal or corrected-to-normal visual acuity. Participants provided written informed consent before being included in the experiment, and all experimental procedures were reviewed and approved by the Institutional Review Board in accordance with the principles of the Declaration of Helsinki.

Experimental Setup

The experimental setup consisted of a rectangular box (60 cm high, 90 cm wide, and 75 cm deep). Stimuli were displayed on a 21-in. CRT (1,024 × 768 pixels, 100 Hz) monitor placed upside-down on the top surface of the structure. Participants perceived the projection of the monitor's image on their horizontal workspace thanks to a mirror dividing the apparatus horizontally (mean background luminance after reflection of the monitor's image on the mirror was 3.5 cd/m^2) that prevented direct vision of the hand. The planar (X,Y) coordinates of the right-hand pointing movements were recorded through an electromagnetic stylus held by the participant (Grip Pen Intuos 3 ZP-501E) on a digitizer tablet (Wacom Intuos 3 PTZ-1231W, A3 size) placed horizontally in the workspace. The participant's head rested on a chin and forehead support tilted toward the mirror plane at a 30° angle. The experimental room was in darkness during the whole experiment. Stimulus display and response recording were controlled with MATLAB 7.6.0. software and the Psychophysics Toolbox (PTB-3; Brainard 1997; Pelli 1997).

Stimuli

Two spatial landmarks were displayed on the screen, indicating the manual response starting position and the visual fixation point (see Fig. 1). The starting position [2-pixel-diameter black dot (0.09° of visual angle), 100% contrast with respect to the background] was displayed at the location corresponding to the stylus' physical starting zone. The fixation point [4-pixel-diameter black dot (0.19° of visual angle), 100% contrast] was located 6.5 cm (7.72° of visual angle) above the starting position along the body midline. Stimuli were presented inside two 1-cm × 1-cm (1.19° × 1.19°) empty black square frames (1-pixel thickness) whose center was located 6 cm (7.16° of visual angle) to the right or left of the fixation point, i.e., at ±45° with respect to the body midline from the starting position. The target (a 100% luminance contrast red patch) randomly filled one of the two square frames. The distractor, when presented, was displayed in the square frame opposite to the target. It was a white Gaussian luminance blob (standard deviation of 0.3°) with a luminance adjusted to yield a perceptual sensitivity (d') close to perceptual threshold. The target and distractor were presented for 10 ms.

A backward mask characterized by one of four noise levels was used to keep the distractor's visibility constant while manipulating its contrast with respect to the background. Noise levels were defined according to the luminance contrast of the pixels of the mask, each of them being randomly selected between ±0% (no mask), ±33%, ±66%, or ±100% of the background mean luminance (3.5 cd/m^2). The mean luminance of each mask was, however, equal to the background luminance. The mask was displayed in both frames for 150 ms immediately after the stimuli (target alone or target and distractor) presentation.

Procedure

Participants performed 700 trials in each mask noise level condition: 100 familiarization trials designed to establish individual RT distribution and to foster participant production of fast motor re-

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[1] This effect was observed for the few participants characterized by the highest detection threshold who were therefore presented with the highest distractor contrast at any given visibility level (i.e., d'). No effect was observed on the manual reaching trajectories.

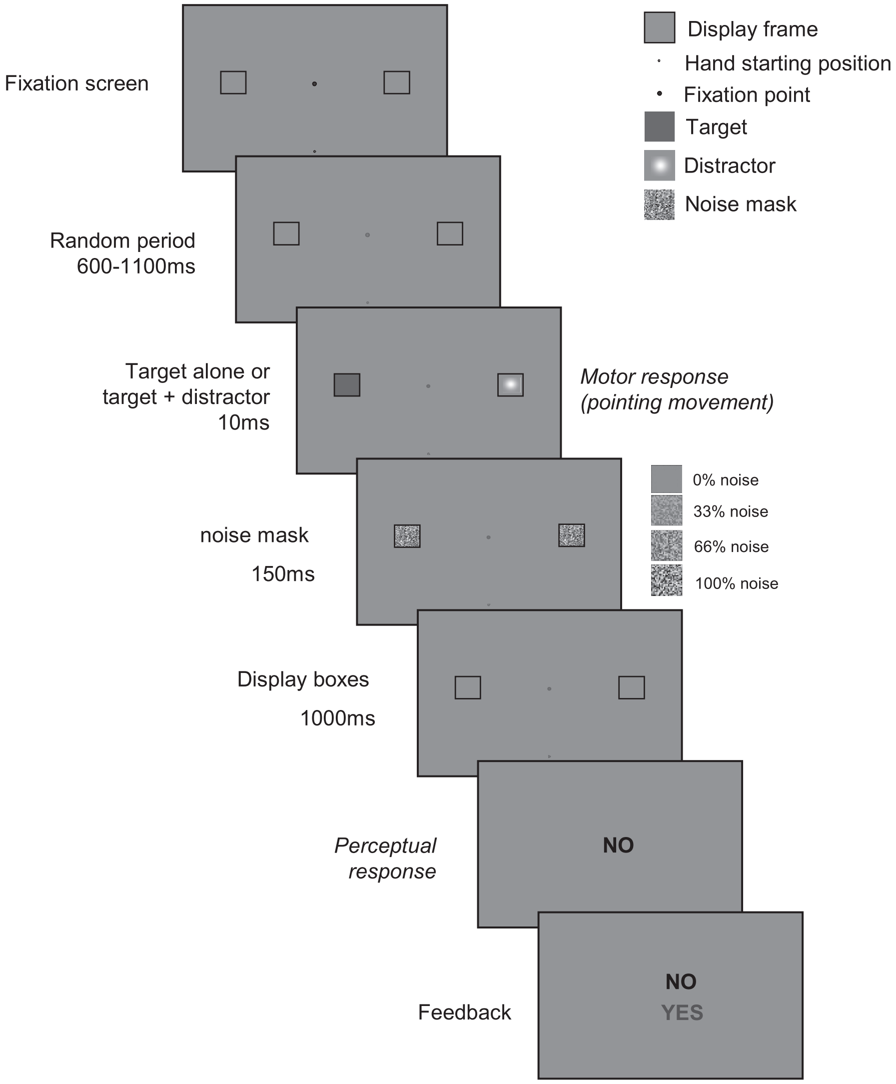

Fig. 1. Temporal sequence of stimuli presentation and participants' responses.

sponses; 300 contrast adjustment trials used to assess, in each participant, the four distractor luminance contrasts yielding a close-to-threshold distractor visibility over the four contrast levels of the backward mask[2]; and 300 trials in each of the four main experimental blocks (see below). Experimental blocks lasted ~80 min and were counterbalanced across the participants in four different sessions.

At the beginning of each trial, participants positioned the stylus on the tablet location corresponding to the visual starting point, using their right hand. They then clicked on the stylus button to start the trial. The contrast of the starting and fixation dots, initially set at 100% contrast, dropped after 100 ms to 50% contrast to cue the beginning of the trial. After a random period of 500–1,000 ms, the target alone or both the target and the distractor were displayed for 10 ms. The target appeared randomly within either the left or right square frames. In 50% of the trials, the distractor appeared in the other frame. The noise mask (0%, 33%, 66%, or 100% contrast) was then immediately displayed in both square frames for 150 ms (Fig. 1). The square frames remained visible for another 1,000 ms, a period of time during which the participant had to perform a fast but accurate pointing movement toward the target location. Participants were instructed to maintain their gaze on the fixation dot until the manual response was provided. After the speeded motor response (provided that the RT lasted between 150 ms and the 95th percentile of the RT distribution individually assessed in the familiarization trials), participants indicated whether or not they detected the distractor. Feedback about the actual presence of the distractor was then displayed on the computer screen (see Fig. 1) to prevent participants from adopting a conservative strategy consisting in systematically answering "no" when they were not fully confident about the presence of the distractor. In other words, providing this feedback was expected to reduce the response bias (i.e., to yield a response criterion, *c*, close to optimal).

Data Recording and Analysis

Perceptual sensitivity and response bias. Perceptual responses were classified as Hits, Misses, False Alarms (FAs), and Correct Rejections (CRs). The overall sensitivity (d') and response criterion (c) of each participant were then computed for each contrast condition.

Spatial and temporal performances of motor responses. Hand movement trajectory was sampled at a frequency of 200 Hz with a spatial definition of 0.01 mm (0.012° of visual angle). The onset of hand movement was defined as the last point in time before the hand's

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[2] During the 100 first trials, the contrast of the distractor varied according to a 1-up 2-down staircase procedure (Levitt 1971) with a contrast increment/decrement step of 1%. In the remaining 200 trials, the contrast of the distractor was randomly selected within an [−2%, +2%] interval (5 different contrasts at steps of 1%) computed from the lowest contrast value obtained between the 90th and the 100th preceding trials. The contrast leading to the d' closest to 1.5 was then selected for each level of noise mask and for each participant.

instantaneous velocity exceeded 20 mm/s. The offset of the movement was defined as the first point in time at which hand velocity dropped below the same velocity threshold. RT and movement time (MT) were computed according to these temporal landmarks. Pointing movement direction was computed by calculating at three different points along the hand trajectory progression the angle of the vector defined by the hand starting position and the hand position at *1*) 20% of the covered trajectory[3] (initial angle, iA), *2*) peak hand velocity[4] (peak velocity angle, pA), and *3*) movement end point (terminal angle, tA) (see Fig. 2). Movements' angular values were then transformed into signed angular errors (AEs) by subtracting the angular value obtained in the Hit, Miss, and FA trials from the angular value obtained in CR trials (baseline) for each participant. Similarly, RTs and MTs were normalized with respect to those obtained in CR trials: the value measured on each Hit, Miss, or FA trial was subtracted from the average CR value for the same target position. A total of 139 pointing movements (1.45% of the movements) were also discarded from the analysis, as the iAE of these movements was larger than 45° when compared with the baseline (CR). Statistical comparisons of experimental conditions were performed with repeated-measures ANCOVAs for testing the effect of the experimental factors including the distractor contrast as a continuous predictor. ANOVAs were also used for testing the effect of the masks in the baselines, and post hoc Scheffé tests were used for local comparisons.

RESULTS

Summary of Results

Data analyses revealed that hand reaching movements (motor responses) deviated toward the distractor when the latter was physically present and detected at all contrasts (Hit trials) and when it remained undetected (Miss trials), although to a lesser extent (leading to close to zero deviations at low contrasts). These deviations increased then with the contrast of the distractor and were larger at the beginning of the movement than halfway or at the end of movement execution (iAEs $>$ pAEs $>$ tAEs). These effects were not observed in FA trials. Finally, the presence of the distractor did not affect RTs or MTs. Results are detailed below.

Discarded Trials

On average, 3.81% of trials (range: 0–15% per session) were discarded because of out-of-range RTs (i.e., $<$150 ms or longer than 95th percentile of RT distribution obtained in familiarization trials). RTs were computed online, and the nonvalid trials were repeated at the end of each session. Among these nonvalid trials, 97.8% were late or no-go motor responses and 2.2% were anticipations. Furthermore, an additional 3.27% of trials were discarded from off-line analysis because participants did not start their pointing movements from the starting zone or took the stylus off the tablet during movement execution.

Distractor Contrasts, Perceptual Sensitivity, and Decision Criteria

Table 1 presents for each of the eight participants and for the four mask conditions the percentage of Hit and FA trials, d', and decision criteria (c) measured in the main experiment. The distractor contrast values used for each participant across the four masking conditions are also reported. The contrast of the distractor varied significantly across the four mask conditions [1-way repeated-measures ANOVA: $F(3,21) = 266.44$, $P < 0.01$; Scheffé post hoc tests $P < 0.01$ for each paired comparison; means over participants were 22.7%, 35%, 46.4%, and 66.4% contrast], while d' value was kept approximately constant across the distractor contrasts [average d': 1.476; repeated-measures ANCOVA: $F(1,30) = 0.27$, $P = 0.61$] and mask contrasts [repeated-measures ANOVA on pooled data across mask contrasts: $F(3,21) = 0.62$, $P = 0.61$]. In other words, the contrast of the distractor varied significantly across the mask conditions but its visibility remained unaffected. Also, c value did not vary significantly as a function of the contrast of the distractor [average c: 0.03; repeated-measures

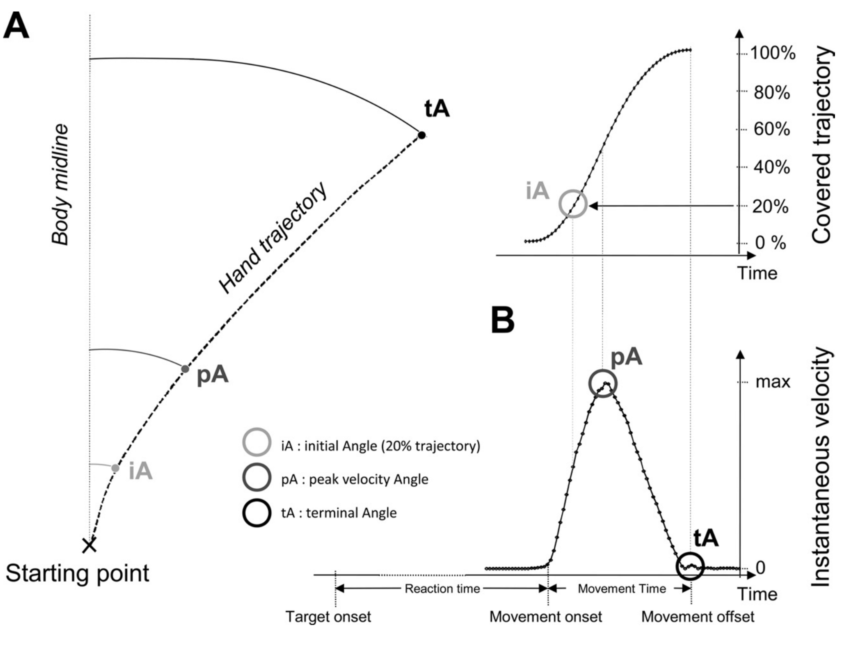

Fig. 2. *A*: example of a typically curved pointing movement with the points at which initial (iA), peak velocity (pA), and terminal (tA) angles were computed. *B*, *top*: iA corresponds to the angle at 20% of the covered trajectory. *Bottom*: pA and tA were defined according to instantaneous velocity. Initial (iAE), peak velocity (pAE), and terminal (tAE) angular errors in Hit, Miss, and False Alarm (FA) trials were then calculated by subtracting from these angles the corresponding (right or left) average angles measured for Correct Rejection (CR) trials (baseline).

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[3] The point on the trajectory used to compute initial angular error corresponded to 20% of the trajectory. Taking an earlier point would have led to artificially enhanced spatial inaccuracies due to the small path covered by the hand before reaching the first 20% of the trajectory.

[4] Peak velocity was on average reached at 34.71% (SD 4.3, range 28.11–49.35%) of the covered trajectory.

Table 1. *Perceptual sensitivity, criterion, percentage of Hits and False Alarms, and distractor's contrast used*

Subjects	d'	c	%H	%FA	ct
		Mask contrast = 0%			
1	1.74	0.1	78.0	16.7	29
2	1.41	0.04	74.7	22.7	24
3	1.24	0.24	64.7	19.3	23
4	1.26	0.16	68.0	21.3	22
5	1.74	−0.1	83.3	22.0	24
6	1.35	0.05	73.3	23.3	21
7	1.33	0.08	72.0	22.7	20
8	1.48	0.31	66.7	14.7	19
All	1.45	0.11	72.6	20.3	22.7
SD	0.2	0.13	6.2	3.17	3.11
		Mask contrast = 33%			
1	1.59	0.05	77.3	20.0	44
2	1.19	−0	72.7	28.0	34
3	1.66	−0.1	81.3	22.0	33
4	1.40	0.1	72.7	21.3	34
5	1.27	−0.1	75.3	28.0	36
6	1.35	0.01	74.7	24.7	34
7	1.48	0.01	76.7	22.7	31
8	1.44	0.25	68.0	16.7	34
All	1.42	0.04	75	22.9	35.0
SD	0.16	0.1	3.93	3.89	3.89
		Mask contrast = 66%			
1	1.49	0.14	72.7	18.7	57
2	1.85	0.13	78.7	14.7	43
3	1.77	−0.11	84.0	22.0	43
4	1.29	0.08	71.3	23.3	47
5	1.45	−0.14	80.7	28.0	45
6	1.57	−0.3	86.0	31.3	43
7	1.76	−0.01	81.3	19.3	42
8	1.19	−0.01	72.7	28.0	51
All	1.54	−0.03	78	23.2	46.4
SD	0.24	0.15	5.59	5.63	5.21
		Mask contrast = 100%			
1	1.62	−0.1	81.3	23.3	78
2	1.41	−0	77.3	25.3	64
3	1.31	0.37	61.3	15.3	69
4	1.46	−0	77.3	24.0	61
5	1.77	−0.2	86.0	24.7	64
6	1.64	−0	80.0	21.3	57
7	1.51	−0.1	80.7	26.0	63
8	1.24	0.1	74.7	22.0	75
All	1.49	0.00	77	22.8	66.4
SD	0.17	0.17	7.29	3.39	7.13

Values are perceptual sensitivity (d'), criterion (c), percentage of Hits (%H) and False Alarms (%FA), and distractor's contrast (ct) used for each participant and each masking condition. Distractor's contrast is expressed in additional percentage according to the background luminance. Participants performed a total of 150 trials without distractor (entailing either a Hit or a Miss) and 150 trials with a distractor (entailing a False Alarm or a Correct Rejection).

ANCOVA with distractor contrast as continuous predictor: $F(1,30) = 1.65$, $P = 0.21$] or the mask conditions [repeated-measures ANOVA on pooled data across mask contrasts: $F(3,21) = 2.03$, $P = 0.14$], indicating that participants' response strategy remained constant across the experimental conditions.

Angular Errors

For each participant and each Hit, Miss, and FA trial, AEs were computed at the initial (iAEs), peak velocity (pAEs), and terminal (tAEs) hand position points and were computed by subtracting pointing angles obtained in each Hit, Miss, and FA trial from the corresponding (right or left) average angle measured in CR trials (baseline, see above). Figure 3 plots the effects of contrast and perceptual state on AEs.

Baseline (correct rejections). Considering all participants and all conditions, mean absolute initial, peak velocity, and terminal pointing angles for CR trials (baseline) were 36.22° (SD 5.53), 36.84° (SD 5.02), and 38.87° (SD 5.16), respectively, with respect to the body midline. A repeated-measures ANCOVA with distractor contrast as continuous predictor revealed that these baseline pointing angles did not vary as a function of the contrast [$F(1,30) = 0.01$, $P = 0.92$] but depended on the point in the trajectory progression: mean terminal angle was greater than mean initial and peak velocity angles [$F(2,60) = 14.60$, $P < 0.01$; Scheffé tests $P < 0.01$]. To ensure that these baselines were not affected by the contrast of the mask itself, we also performed a two-way repeated-measures ANOVA on pointing angles grouped by mask condition [mask condition: $F(3,21) = 0.15$, $P = 0.93$; point in trajectory progression: $F(2,14) = 14.60$, $P < 0.01$]. Such slight trajectory curvature has been extensively reported for natural hand movements (Boessenkool et al. 1998; Miall and Haggard 1995; Osu et al. 1997; Wolpert et al. 1994) and may be attributed to motor response optimization for minimizing end point variability (Harris and Wolpert 1998).

Hit, Miss, and FA trials. Relative AE (i.e., with respect to CR trials) statistics for Hit, Miss, and FA trials were performed with a repeated-measures ANCOVA with point in trajectory progression (iAEs, pAEs, tAEs) and response category (Hit, Miss, FA) as main factors and distractor contrast as continuous predictor. Means and standard deviations for the group's performances are presented in Fig. 3. Statistical analyses revealed that AEs were larger in Hit than in Miss trials and in Miss than in FA trials [$F(2,60) = 54.99$, $P < 0.01$; all Scheffé paired comparisons $P < 0.01$] and progressively decreased during the completion of the movement [$F(2,60) = 3.87$, $P < 0.05$; all Scheffé paired comparisons $P < 0.01$], with no interaction between these two factors [response category × point in

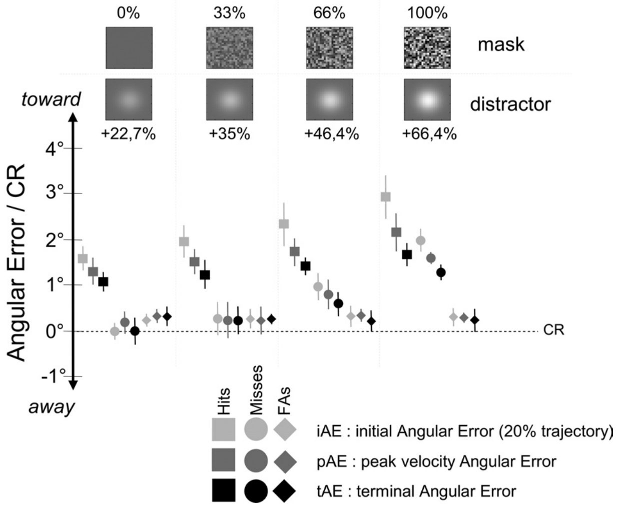

Fig. 3. iAEs, pAEs, and tAEs according to the CR trials for Hit, Miss, and FA trials. Positive and negative values are AEs toward and away from the distractor, respectively. Each symbol represents the mean performance for the 8 participants. Error bars show SD.

trajectory progression: $F(4,120) = 1.88$, $P = 0.12$]. We also found that AEs increased with the contrast of the distractor [$F(1,30) = 281.82$, $P < 0.01$], this effect varying with the category of response [response category × contrast interaction: $F(1,30) = 57.73$, $P < 0.01$]. Indeed, the effect was present at all the points in trajectory progression in Hit and Miss trials (univariate statistics: $P < 0.01$ for iAE, pAE, and tAE) but absent in FA trials (univariate statistics: $P > 0.13$ for iAE, pAE, and tAE). It is also noteworthy that deviations toward the distractor were significantly larger than the baseline even for low contrasts in Hit trials (t-test with respect to the baseline, 0, considering pooled data across participants in the 22.7% contrast condition: $P < 0.01$ for iAE, pAE, and tAE) but were not different from the baseline in Miss trials (t-tests: $P > 0.18$ for iAE, pAE, and tAE). AEs were, however, significantly different from the baseline for both Hit and Miss trials for the highest contrasts [66.4% contrast condition (mean for the group): t-test with respect to the baseline, all $P < 0.01$].

In short, these results indicate that *1*) a present and detected distractor (Hit trials) had a compulsory effect on motor responses that increased with the contrast of the distractor; *2*) such an effect was also observed with an undetected distractor (Miss trials), but to a lesser extent—deviations being thus close to zero at low contrasts; *3*) deviations were larger at the beginning of the pointing moments and decreased through the completion of the moment; and *4*) no such effects (*1*, *2*, and *3*) were observed in FA trials, i.e., when the distractor was absent but detected (FA trials).

Reaction Times

RTs in Hit, Miss, and FA trials were computed relative to the mean RTs obtained in CR trials for each participant in each contrast condition. These RT differences were then analyzed by means of a repeated-measures ANCOVA [main factor: perceptual response category (Hits, Misses, FAs); continuous predictor: distractor contrast].

Baseline (correct rejections). Mean RT over all the participants and conditions was 255.66 ms (SD 37.16 ms). Mean RTs in the 22.7%, 35%, 46.4%, and 66.4% mask contrast conditions were 251.12 ms (SD: 35.87 ms), 254.12 ms (SD: 37.36 ms), 258.37 ms (SD: 37.74 ms), and 259.00 ms (SD: 44.27 ms), respectively. Individual RT baselines did not vary as a function of the individual contrast of the distractor [ANCOVA: $F(1,30) = 0.46$, $P = 0.50$] or the mask condition when pooling the data for the group [ANOVA: $F(3,21) = 0.16$, $P = 0.92$].

Hit, Miss, and FA trials. Analysis of relative RTs in the Hit, Miss, and FA trials did not show any effect of either response category [$F(2,60) = 0.24$, $P = 0.79$] or contrast of the distractor [$F(1,30) = 0.21$, $P = 0.65$]. Such RT independence from both distractor contrast and perceptual response category was expected given that the target contrast was constant and that the visibility of the distractor was also constant whatever its contrast. Similar results showing trajectory deviations in the presence of distractors without influence on RTs have already been reported for both near-threshold (Cardoso-Leite and Gorea 2009) and suprathreshold (Welsh et al. 1999) stimuli.

Movement Times

The statistical analysis was similar to that used for RTs.

Baseline (Correct Rejections). Mean MT for CR trials was 292.3 ms (SD 33.84 ms) and 297.62 ms (SD 43.05 ms), 302 ms (SD 29.61 ms), 284.94 ms (SD 31.02 ms), and 284.63 ms (SD 33.31 ms) in the 22.7%, 35%, 46.4%, and 66.4% contrast conditions, respectively. Individual MT baselines did not vary as a function of the individual contrast of the distractor [ANCOVA: $F(1,30) = 2.87$, $P = 0.10$] or the mask contrast when pooling all the data [ANOVA: $F(3,21) = 0.16$, $P = 0.92$].

Hit, Miss, and FA trials. A repeated-measures ANCOVA (main factor: response category; continuous predictor: distractor contrast) did not reveal any effect of the response category [$F(2,60) = 0.92$, $P = 0.40$] or the contrast of the distractor [$F(1,30) = 3.09$, $P = 0.09$] on MTs.

DISCUSSION

The purpose of the present study was to evaluate in a manual reaching task the effect of a near-threshold distractor of variable contrast but fixed visibility on the relation between the detection of this distractor and the early visual process responsible for trajectory deviations of hand-to-target movement toward this distractor. In four experimental conditions yoking four backward mask contrasts (0%, 33%, 66%, and 100%) with four distractor contrasts (22.7%, 35%, 46.4%, and 66.4% when averaged across participants) so as to keep each participant's distractor sensitivity constant and close to the perceptual threshold, participants performed fast pointing movements toward a highly visible target and subsequently provided, on each trial, a perceptual judgment on the presence/absence of the near-threshold distractor presented in 50% of the trials at a position symmetrical to that of the target along the horizontal meridian.

Previous models of visual target selection for action are consistent in considering how the processing of a visual distractor leads to hand-to-target trajectory deviations toward or away from this distractor (Tipper et al. 1997, 2001; see also Arai and Keller 2005; Godijn and Theeuwes 2002; Quaia et al. 1998; Song and Nakayama 2006, 2008; Walton et al. 2005). According to these models, target selection depends on spatially localized activations in a visuomotor map where the activities generated by the presence of a target and a distractor are merged to provide the terminal end point of the movement. For short-RT responses (McSorley et al. 2006), as in the present study, end point specification is assumed to be based on early excitatory processes leading to a shift of movement end point toward the distractor (the well-known "global effect"; see Findlay 1982; Sailer et al. 2002). By contrast, longer RTs (i.e., >200 ms) lead to a deviation away from the distractor, possibly due to a reactive inhibition of the irrelevant distractor-triggered activity (McSorley et al. 2006; Tipper et al. 2001).

Accordingly, deviations toward the distractor were observed in the present study when the participants were prompted to respond with short RTs, i.e., when focusing on the early visual processing involved in target selection (McSorley et al. 2006). Also, we found that trajectory deviations were larger at hand movement onset and decreased along the progression of the movement. This supports the notion that while the movement's initial programming was biased toward the distractor (Arai and Keller 2005; Godijn and Theeuwes 2002; Quaia et al. 1998; Song and Nakayama 2006, 2008; Tipper et al. 2001; Walton et al. 2005), fast midflight trajectory corrections occurred as the movement unfolded (Fautrelle et al. 2010; Song and Nakayama 2006, 2008). According to this interpretation, it is noteworthy that the appearance of the mask in both frames could have reduced target salience and then contributed to strengthen distractor effect on manual performances. Indeed, it has been shown that reducing stimulus salience has an effect on both RT (e.g., Bell et al. 2006) and MT (Zehetleitner et al. 2011). However, since in our experiment RTs and MTs (or even movement angles) did not differ with respect to the masking conditions in the CR trials (baseline), one may plausibly consider that deviation effects in Hit and Miss trials depend on the distractor's contrast rather than on the reduction of target salience.

The critical finding of the present study is then that the deviation toward the distractor depended on both the participant's perceptual state and the distractor contrast, despite the fact that the visibility (d') of the distractor was kept constant. Indeed, pointing movements deviated toward the distractor when the latter was detected (perceptual Hits) for all distractor contrasts—including low contrasts, although the deviations observed in the presence of an undetected distractor (Miss trials) were close to zero at low contrast levels (see Fig. 3). As previously noted on the basis of data obtained with similar experimental paradigms measuring manual RTs (Waszak et al. 2007; Waszak and Gorea 2004), saccade trajectories (Cardoso-Leite et al. 2009), or manual trajectories (Deplancke et al. 2010), the lack of effect of nonperceived, though available, visual stimuli on motor behavior challenges the dominant perception-action model according to which visual stimulation is processed independently along two distinct pathways for conscious perception and for action (see, e.g., Goodale 2011; Westwood and Goodale 2011). Instead, the present data suggest a strong visuo-motor coupling similar to what has been previously reported in a number of other experimental studies involving visual illusions (e.g., Franz and Gegenfurtner 2008), temporal order judgments (Cardoso-Leite et al. 2007), image classification (e.g., Eckstein et al. 2007), motion perception and pursuit eye movements (e.g., Debono et al. 2012), or perception and action in a three-dimensional environment (Knill and Kersten 2004; for review, see Cardoso-Leite and Gorea 2010).

In apparent contrast with these studies, however, we also found in the present experiment that undetected visual stimuli can affect motor behavior, providing that the visual stimulus was presented at high luminance contrasts while maintaining its visibility constant and close to the perceptual threshold by means of backward masking. This observation indicates that dissociation between perceptual and motor responses can be obtained, providing that the undetected visual information itself, either masked or not, reaches a sufficient contrast level. These data thus generalize to previous complex motor behavior observations made by Waszak et al. (2007), who found a similar pattern of results with RT measurement. Interestingly, the common point between these two studies and the others reporting a subliminal effect of visual stimulation on the action system (Amundson and Bernstein 1973; Binsted et al. 2007; Cressman et al. 2007; Ogmen et al. 2003; Taylor and McCloskey 1990; Van der Stigchel et al. 2009) is precisely the use of high-contrast, strongly masked distracting stimuli. In line with this, all studies that failed to show an impact of subliminal stimulations on motor behavior used low-contrast distractors either with or without visual masks (Deplancke et al. 2010; Cardoso-Leite et al. 2009; Waszak et al. 2007; Waszak and Gorea 2004). Thus, as previously pointed out (Bruno et al. 2010; Cardoso-Leite and Gorea 2010; Smeets and Brenner 2006), the outcome of experiments bearing on the relation between perceptual and motor processes depends on a number of experimental design features such as the nature of the perceptual and motor tasks, the response modes, and, as shown in the present study, the contrast of the interfering stimuli.

The contrast-dependent perceptuo-motor coupling vs. dissociation presently observed can be accounted for by a model in which perceptual and motor decisions are based on the same incoming signal but referenced to distinct decisional thresholds or criteria (Miller and Schwarz 2006; Waszak et al. 2007; Waszak and Gorea 2004). In the context of the present paradigm, such a model posits that perceptual and motor decisions are differentially modulated by the presence of a mask of variable contrast. On one hand, as the perceptual task requires comparison of visual activations elicited by the mask alone and by the mask plus distractor, perceptual decisions must be taken with reference to a relatively high visual activation regime elicited by the highly suprathreshold mask. On the other hand, the motor response should be triggered anytime the visual activation elicited by the (also suprathreshold) target exceeds a decision criterion referenced to the absence of any visual activity and hence substantially lower than the perceptual criterion. Consequently, the visual activation elicited by a high-contrast, strongly masked distractor might be sufficiently strong to exceed the motor threshold (and thus to influence the motor response) but not strong enough to exceed the perceptual criterion (thus entailing a perceptual miss in some trials). The consequence of this particular activation state would thus translate into a perceptual-motor "dissociation." With lower mask and distractor contrasts, the perceptual criterion will be set at a lower visual activation level so that the distractor-triggered activation failing to exceed this criterion (a perceptual miss) will also fail to exceed the motor criterion. No impact on the motor response will be observed in this case, thus revealing a perceptual-motor "coupling." According to this interpretation, the observed visuo-motor "dissociation"/"coupling" duality is the consequence of how visual information is processed depending on the contrast level of the stimuli and the requirements of the task.

Current neurophysiological models of visual masking (Breitmeyer and Ganz 1976; Lamme 1995; Macknik and Livingstone 1998) may account for the present data in a complementary way. According to these models, the early neuronal response to a visual stimulus (e.g., a distractor) consists of two successive neural components: a first stimulus-dependent component, presumably processed through a transient feedforward sweep of activation, and a second perception-dependent component consisting in a sustained reentrant activation from higher cortical areas (for recent discussions see Breitmeyer 2007; Macknik and Martinez-Conde 2007, 2009; Super and Lamme 2007). Within this framework, backward visual masking presumptively suppresses the sustained perception-dependent neuronal response without affecting the stimulus-dependent feedforward activity related to the masked stimulus, hence reducing the visibility of the latter while still allowing its unconscious processing.[5]

Accordingly, the presently observed trajectory deviations toward the undetected (Miss trials) high-contrast, strongly masked distractor would result from the influence, on target selection, of the strong transient feedforward activation elicited by this high-contrast distractor. This transient activation would remain unaffected by the backward mask despite the induced drop in visibility. On the contrary, the absence of trajectory deviations in the presence of an undetected low-contrast, slightly masked distractor would be explained by its related transient activation being too weak to drive the motor response automatically. Interestingly, the fact that trajectory deviations were always present in the presence of a detected—even low contrast—distractor (Hit trials) can also be accounted for by such a neurophysiological approach. Indeed, it has been suggested that the main role of the feedback projections mediating the sustained (perception dependent) component of the neuronal response is to modulate the initial feedforward sweep of activation associated with the presence of the stimulus (de Lafuente and Romo 2005; Macknik and Martinez-Conde 2007, 2009; Super and Lamme 2007). In other words, the neuronal activation associated with a "seen" perceptual response would act as a gain applied to the activation related to the stimulus' presence, thus leading to a compulsory effect of a present and detected distractor on motor control. Conversely, such enhancement would not lead to a motor interference in FA trials, as even if the "seen" modulatory activation is at work when a fictive distractor is perceived, such modulation could not be applied to the activation related to the stimulus' physical presence. Besides, such enhancement mechanism is upheld by the dense interconnections between stimulus-related and percept-dependent areas (Deco and Romo 2009; de Lafuente and Romo 2005; Macknik and Martinez-Conde 2009; Ress and Heeger 2003) and by the similar conduction speeds of both feedforward sweep and feedback activations linking these areas (Girard et al. 2001).

To summarize, showing that a nonperceived stimulus can affect motor behavior has been used as a critical test for probing the dissociation between a conscious vision for perception and an unconscious vision for action within the visual system. The present study clearly shows that interpretation of empirical data within this theoretical framework is not trivial, as it highlights the crucial role of the experimental condition under which the test is performed. Specifically, data obtained in the present study (together with previous RT studies; Waszak et al. 2007; Waszak and Gorea 2004) revealed a strong perception-action coupling (i.e., motor responses not being affected by unseen distractors) when using visual stimuli with low contrasts, and a perception-action dissociation (i.e., motor responses being affected by unseen distractors) when using visual stimuli with high contrasts. As discussed above, these different patterns of results can be accounted for by complementary models: a behavioral model considering that perceptual and motor decisions are based on distinct, task-dependent, perceptual and motor decision criteria and a neurophysiological model positing a fast transient feedforward sweep of activation subsequently modulated by a sustained reentrant feedback activation linked to the stimulus perception. These two compatible theoretical frameworks underline the contribution of both stimulus-related and perception-dependent activations in target selection for action, thus strengthening the conception of a tight link between perception and action at the early stages of visual processing. Thus, although it is acknowledged that the visual system uses different pathways for high-level visual processing, the present study suggests that dissociation between conscious vision for perception and unconscious vision for action may be also accounted for by signal modulations at the very early stages of visual processing.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: A.D., L.M., A.G., and Y.C. conception and design of research; A.D. performed experiments; A.D., L.M., and Y.C. analyzed data; A.D., L.M., A.G., and Y.C. interpreted results of experiments; A.D. prepared figures; A.D., L.M., A.G., and Y.C. drafted manuscript; A.D., L.M., A.G., and Y.C. edited and revised manuscript; A.D., L.M., A.G., and Y.C. approved final version of manuscript.

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[5] It is noteworthy that Macknik and Martinez-Conde (2007, 2009) consider that the second component of the response reflects the transient activation related to the stimulus offset instead of the sustained reentrant activation linked to the stimulus awareness (Breitmeyer 2007; Super and Lamme 2007). These two positions are not incompatible, since even if the second neural component of the response corresponds to the stimulus offset transient activity, this component is empirically correlated to the stimulus awareness in the case of backward masking.

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