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Comparison of Perceptual and Motor Decisions Via Confidence Judgments and Saccade Curvature

Pedro Cardoso-Leite and Andrei Gorea

Laboratoire Psychologie de la Perception, Université Paris Descartes and Centre National de la Recherche Scientifique, Paris, France

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Cardoso-Leite P, Gorea A. Comparison of perceptual and motor decisions via confidence judgments and saccade curvature. *J Neurophysiol* 101: 2822–2836, 2009. First published March 4, 2009; doi:10.1152/jn.91269.2008. This study investigated the effects on perceptual and motor decisions of low-contrast distractors, presented 5° on the left and/or the right of the fixation point. Perceptual decisions were assessed with a yes/no (distractor) detection task. Motor decisions were assessed via these distractors' effects on the trajectory of an impending saccade to a distinct imperative stimulus, presented 10° above fixation 50 ms after the distractor(s). Saccade curvature models postulate that distractors activate loci on a motor map that evoke reflexive saccades and that the distractor evoked activity is inhibited to prevent reflexive orienting to the cost of causing a saccade curvature away from the distractor. Depending on whether or not each of these processes depends on perceptual detection, one can predict the relationships between saccades' curvature and perceptual responses (classified as correct rejections, misses, false alarms, and hits). The results show that saccades curve away from distractors only when observers report them to be present. Furthermore, saccade deviation is correlated (on a trial-by-trial basis) with the inferred internal response associated with the perceptual report: the stronger the distractor-evoked perceptual response, the more saccades deviate away from the distractor. Also in contrast with a supersensitive motor system, perceptual sensitivity is systematically higher than the motor sensitivity derived from the distributions of the saccades' curvatures. Finally, when both distractors are present (and straight saccades are expected), the sign of saccades' curvature is correlated with observers' perceptual bias/criterion. Overall the results point to a strong perceptual-motor association.

INTRODUCTION

A major challenge in cognitive sciences is the appraisal of the relationship between perception and action and of the subtending biological processes (Glimcher 2003). Here we address this general issue by investigating the link between the subjective visibility of close to threshold distractors and the trajectory of saccades directed to a highly visible target.

Perceptual and motor decisions

According to a popular view, action and perception are independent (Goodale and Milner 1992; Milner and Goodale 1995). This view was originally supported by evidence from neuropsychology (for a review, see Milner and Goodale 1995) and from the observation of differential effects of visual illusions on perceptual and motor responses (e.g.,

Aglioti et al. 1995; Haffenden and Goodale 1998). Such evidence has been firmly contested (Dassonville and Bala 2004; Franz and Gegenfurtner 2008; Franz et al. 2000; Rossetti et al. 2003; Schenk 2006). Additional support of the perception-action dissociation came from studies that used allegedly “invisible” primes and showed that, despite their “invisibility,” they can modulate the motor responses (Fehrer and Raab 1962; Klotz and Neumann 1999; Mulckhuyse et al. 2007; Neumann 1982; Taylor and McCloskey 1990; Vorberg et al. 2003; Waszak and Gorea 2004; Waszak et al. 2007; see also Schmidt and Vorberg 2006). Studies having shown that manipulations of stimulus intensity yield unequal modulations of reaction times and of perceptual latencies (as inferred from a temporal order judgment task) (for reviews, see Jaśkowski 1996, 1999; Sternberg and Knoll 1973) have also been taken to corroborate the perception-action dissociation stand (e.g., Neumann et al. 1993; Steglich and Neumann 2000; Tappe et al. 1994). However, such findings do not undoubtedly imply that perception and action are processed within independent systems. Consistent correlations between perceptual and motor responses suggest that both responses result from a common processing stream with the different perceptual and motor performances resulting from two distinct decisions taken successively on a unique internal signal according to the likelihood of the stimulus' presence over time (Waszak and Gorea 2004; Waszak et al. 2007). That perceptual and motor behaviors are based on the same evoked internal response has also been sustained by image classification (Beutter et al. 2003; Eckstein et al. 2007) and ocular pursuit (Osborne et al. 2005; Stone and Krauzlis 2003) studies. The former demonstrated that the spatial distributions of the sampled information subtending perceptual and motor decisions are close to identical. The latter have shown that pursuit and perception rely on a common representation (but see Gegenfurtner et al. 2003). The rebuttal of the perceptual-motor dissociation is, after all, in accord with the common sense intuition that an optimal interaction with the environment requires the two behaviors be based on the same representation of the external world.

In the present study, we approach the general issue of the relationship between “action” and “perception” by investigating the link between the subjective visibility of close to threshold distractors and the curvature of saccades directed to a highly visible target. In the remainder, we review some results obtained from distinct studies of perceptual detection and of saccade curvature and present their putative relationships when assessed simultaneously.

Address for reprint requests and other correspondence: P. Cardoso-Leite, Laboratoire Psychologie de la Perception UMR 8158, Université Paris Descartes and CNRS, 45 rue des Saints Pères, 75006 Paris, France (E-mail: pdcardoso@gmail.com).

Perceptual detection

Low-contrast stimuli may or may not be reported when presented (yielding respectively perceptual hits and misses), or when absent (yielding, respectively, false alarms and correct rejections). Signal detection theory (SDT) (Green and Swets 1966) considers perception as a statistical decision process where observers evaluate an internal response—possibly firing rates—contingent on stimulus' presence ("signal" trials) or absence ("noise" trials) relative to a decision criterion. Irrespective of the physical stimulation, an internal response below or above the criterion entails a "not seen" or "seen" report, respectively.

Using functional magnetic resonance imaging (fMRI), Ress and Heeger (2003) investigated the human neural correlates in the early visual cortex (V1–V3) of the subjective reports in a yes/no contrast-increment detection task. They observed increased blood-oxygen-level-dependent (BOLD) activity (spatially confined to the retinotopic representations of the stimulus) for perceptual hits and false alarms but not for perceptual misses with correct rejections serving as the baseline. Hence the activity in these areas reflects observers' perceptual state rather than the physical presence of a stimulus. Whether these brain areas cause the perceptual decisions or merely reflect a process that depends on these decisions remains an open question that the low temporal resolution of the fMRI technique does not allow to answer. Neurophysiological studies (Thompson and Schall 1999, 2000) have investigated the neural correlates of the detection of backward masked targets in the macaque frontal eye field (FEF), a structure known for its implication in the control of saccades and in target selection (Schall 2002). The initial response in the FEF (50–100 ms after target onset) reflected the physical presence of the stimulus, whereas the perceptual decision (or awareness) correlated with the delayed FEF activity (100–300 ms after stimulus onset) (see also Lamme and Roelfsema 2000). Inasmuch as this initial response can affect a motor response, these findings are consistent with the view that motor and perceptual decisions are based on the same internal response but are taken sequentially with the perceptual decision requiring more processing time than the motor decision (for a discussion, on this point see Waszak et al. 2007).

Saccade trajectories curve away from irrelevant distractors

Saccades are thought of as ballistic eye movements mainly because of their short duration (~70 ms for 10° amplitude movements) (Leigh and Zee 2006). Their ballistic nature is nonetheless questioned by studies favoring the existence of ongoing oculomotor processes after the saccade initiation (e.g., Carpenter 1988; Gaveau et al. 2003). Indeed saccades are affected by a number of contextual factors, such as target jumps (e.g., van Gisbergen et al. 1987), the presence of distractors close to the target (e.g., Findlay and Harris 1984), prior history (e.g., McPeck et al. 2000), a priori knowledge of target and distractor locations (e.g., Walker et al. 2006), target-distractor similarity (e.g., Ludwig and Gilchrist 2003), or attention (e.g., Sheliga et al. 1994; for a recent review, see Van der Stigchel et al. 2006). Most relevant to the present study is the finding that saccade curvature is affected by the presence of task-irrelevant distractors (Doyle and Walker 2001; McSorley

et al. 2004; Van der Stigchel and Theeuwes 2005; Walker et al. 2006). Doyle and Walker (2001) showed that an irrelevant visual stimulus (distractor), presented simultaneously with the imperative signal (the onset of a peripheral target—eliciting "reflexive" saccades—or the change of the fixation mark into an arrow indicating where to saccade—evoking "voluntary" saccades) makes the saccades curve away from the distractor.

Numerous models have been proposed to account for this "curvature away" effect (Arai and Keller 2005; Godijn and Theeuwes 2002; McSorley et al. 2004; Quaia et al. 1999; Sheliga et al. 1994; Tipper et al. 2001; Walton et al. 2005). All these models assume that the spatially localized activity generated by the mere presence of the distractor irrepressibly "attracts" the saccade toward the distractor. A second mechanism is thus required to explain why and under what conditions saccades curve away from the distractor. The models cited above differ mainly with regards to this second mechanism. Tipper and colleagues (1997, 2001) for instance, proposed a "population coding" model where the saccade target and distractors evoke activations in populations of neurons in a motor map. The weighted average of the activity in that map determines the saccade direction at the moment of saccade initiation. According to this model, the distractors initially evoke an activation that attracts the gaze; this reflexive attraction is then "reactively inhibited," with the strength of this inhibition proportional to the distractor evoked excitation. If target- and distractor-related activities overlap, inhibition of the distractor-evoked activity will truncate the distribution of the target-evoked activity by suppressing the overlapping area. This suppression should cause a shift of the target evoked distribution mean in the direction opposite to the distractor.

A number of neurophysiology studies suggest that the initial excitation is independent of the perceptual state. This stand is based on the observation that FEF neurons show short-latency activations in response to masked stimuli that are not perceptually detected (Thompson and Schall 1999, 2000) and that such FEF activations may trigger saccades possibly via the superior colliculus (Bruce et al. 1985). Electrical stimulation of either of these two structures triggers a saccade in ~30 ms (Bruce et al. 1985). Such results support the notion that the initial excitation postulated by "saccade curvature models" does not subtend "conscious" perception. The relationship between the perceptual state and the inhibitory process is less clear. Thompson and Schall (1999, 2000) found that the perceptual decision correlated with the *delayed* FEF activity (100–300 ms). McPeck (2006) reported that in a visual search task where a target is presented among multiple distractors the amount of activity decrease (relative to a baseline) of FEF neurons responding to an arbitrary distractor correlates with the magnitude of saccade-curvature away from that distractor. Taken together these studies seem to be consistent with the notion that the inhibition process postulated by saccade curvature models correlates with the observer's perceptual state. This conclusion is at odds with Tipper and colleagues' (1997, 2001) hypothesis of a delayed inhibition proportional to the early excitation as such a correlation does not admit the possibility that one of them be related to the perceptual state and the other not. Be it as it may, we know of no study having revealed the temporal unfolding of the two processes as it should be evidenced by a change in the curvature sign during a saccade. It is then possible that these processes be completed

before saccade initiation and yield a net saccade trajectory deviation (as supported by the absence of a correlation between saccade curvature and latency; e.g., McSorley et al. 2004; Walker et al. 2006).

In the present study, we shall consider only the net saccade curvature effect and scrutinize its relationship with the perceptual state evoked by close to threshold perturbing/distracting stimuli. Saccade curvatures will be classified according to observers' yes/no reports concerning the presence of distractors in conjunction with these distractors' actual physical presence, i.e., for perceptual hits, false alarms (FAs), misses and correct rejections (CRs; with the latter used as a reference). On the assumption that saccade deviations away from the distractor depend on observers' perceptual state, they should be observed only on hit and FA trials with no away or toward deviations on miss trials. This would be the case only under Tipper and colleagues' "reactive inhibition" hypothesis provided that the initial excitation process is perceptual state dependent. If this latter condition was not satisfied (i.e., a perceptual state independent excitation process), away deviations should be overall larger on signal (hits and misses) than on noise trials (FA) with deviations toward the distractor never to be observed. On the other hand, going along with the hypothesis that only the delayed inhibition process is perceptual state dependent, one should expect away deviations on hits and FA trials and toward deviations on miss trials.

METHODS

Apparatus

Stimulus presentation and response recordings were controlled under Matlab R14 using the Psychophysics (ptb-3) and the EyeLink Toolboxes (Brainard 1997; Cornelissen et al. 2002; Pelli 1997) (see <http://psychtoolbox.org/>) by an Intel Dual Core computer (2.13 GHz; 2Go RAM). Except for the eye movements, observer's responses were transmitted via the mouse buttons. Stimuli were displayed on a 19-in CRT monitor (1,024 × 768 pixels) with a 120-Hz refresh rate and a mean background luminance of 40 cd/m² (which approximately corresponded to the average illumination of the experimental room). The participant's head was stabilized with a chin and forehead rest at a distance of 57 cm from the monitor. A second computer (Intel Pentium 4, 2.6 GHz; 512 Mo RAM) controlled the registration of the eye movement's data on-line by means of an infra-red video-based eye tracker system (desktop mounted EyeLink 1000; SR Research), which in the monocular recording configuration used has a temporal and spatial resolution of 1,000 Hz and <.01° RMS, respectively.

Stimuli

There were two types of stimuli, the saccade target and the distractors. Both were Gaussian luminance blobs with a SD of 0.3°. The *target* stimulus had a luminance contrast of 20% and was displayed at 10° above the fixation dot along the vertical meridian for ~498 ms (62 frames). The contrast of the *distractors* was determined for each participant separately via a 2AFC procedure so as to yield a *d'* of ~1 [i.e., 76% correct; contrast mean (± SD) across observers = 17.3 ± 0.25%]. When present, distractors were flashed for ~8 ms (1 frame) at 5° eccentricity on the left and/or the right of the fixation dot along the horizontal meridian passing through fixation. Stimulus intensity is known to strongly affect processing latencies (for a review, see Luce 1986; p. 58–64.). Because the distractors were less salient than the target, they were presented 49.8 ms before the target so as to reduce their perceived onsets asynchrony. Note however, that the average target versus distractor detection latency difference has

not been measured. The fixation dot was presented at the center of the screen and had a diameter of 0.2° and a luminance contrast of 100% between trials and of 50% during trials.

Procedure

GENERALITIES. The present study comprises two preliminary and one main experiment. As the main experiment involves a dual task, observers may differ in the way they distribute their resources between the two tasks. The two preliminary experiments were meant to force participants to adopt as much as possible similar ocular response strategies. The first preliminary experiment, referred to as "fast saccades" (see following text), was focused on assessing participants' fastest response to the onset of the *target* stimulus in the absence of distractors. In this condition, participants allocate all their resources to the execution of the saccade. Individual latency distributions were used to determine the feedback rules for the second preliminary experiment, termed "2AFC" (see following text). The 2AFC task was meant to assess the individual contrast values of the distractor corresponding to a detection sensitivity, d_a , of 1 as well as the speeded oculomotor latencies in the presence of distractors so as to calibrate the feedback rules in the main experiment.

In both the preliminary and main experiments, observers started a trial by fixating the 100% luminance contrast central dot; 200 ms after the detection of a correct fixation by the eye tracker (i.e., the presence of the gaze at a location no more than 1° away from the fixation dot), the luminance contrast was reduced to 50% indicating the beginning of the trial. After a fixed 800 ms period followed by a truncated (to a maximum of 2,700 ms) exponentially distributed foreperiod with a mean of 700 ms, the target stimulus appeared 10° above the fixation dot and participants were to saccade as fast and accurately as possible to the target (see Fig. 1A). They were given on each trial visual feedback regarding their saccade latency and landing position error. They also received a score and a "good", "bad", "slow", "anticipation", or "inaccurate" message reflecting their performance in the saccade task (Fig. 1C). Participants were instructed to maximize their cumulative score. The exact feedback rule for the latency criterion differed between conditions although in all of them latencies <100 ms were considered as anticipations (Doyle and Walker 2001; Wenban-Smith and Findlay 1991). Saccades that did not land within 2° about the target were also discarded (Aizawa and Wurtz 1998; Doyle and Walker 2001).

Calibration and validation procedures were performed by the EyeLink software before each 50-trial block and were meant to assess and test the function relating the video image of the eye (diameter of the pupil and IR corneal reflection) to the coordinates of the gaze position on the screen. Observers were asked to saccade to a 1° diam full-contrast disk that randomly jumped to one of nine successive positions. Minimum accuracy requirement was that mean saccade landing position differences between calibration and validation measures were within 0.5°.

PRELIMINARY EXPERIMENT 1: FAST SACCADDES. The aim of this preliminary experiment was to assess the fastest possible saccades that participants could perform in reaction to the target onset. Latencies <100 ms or >300 ms entailed a 100-point loss and were signaled by an "anticipation" or "too slow" message, respectively; messages were displayed in red letters 5° below the fixation dot. For latencies between 100 and 300 ms, the obtained scores decreased linearly with saccade latency from ±100. If observers did not land within 2° about the target, they were given an "inaccurate" message and lost an additional 100 points. If the landing point was ok and the latency yielded a positive score, a "good" message was displayed in green. The 95th percentile of the latency distribution assessed within this condition was used to determine the latency feedback rule of the second preliminary experiment. This fast saccades preliminary experiment consisted in 100 trials and lasted ~10 min per observer.

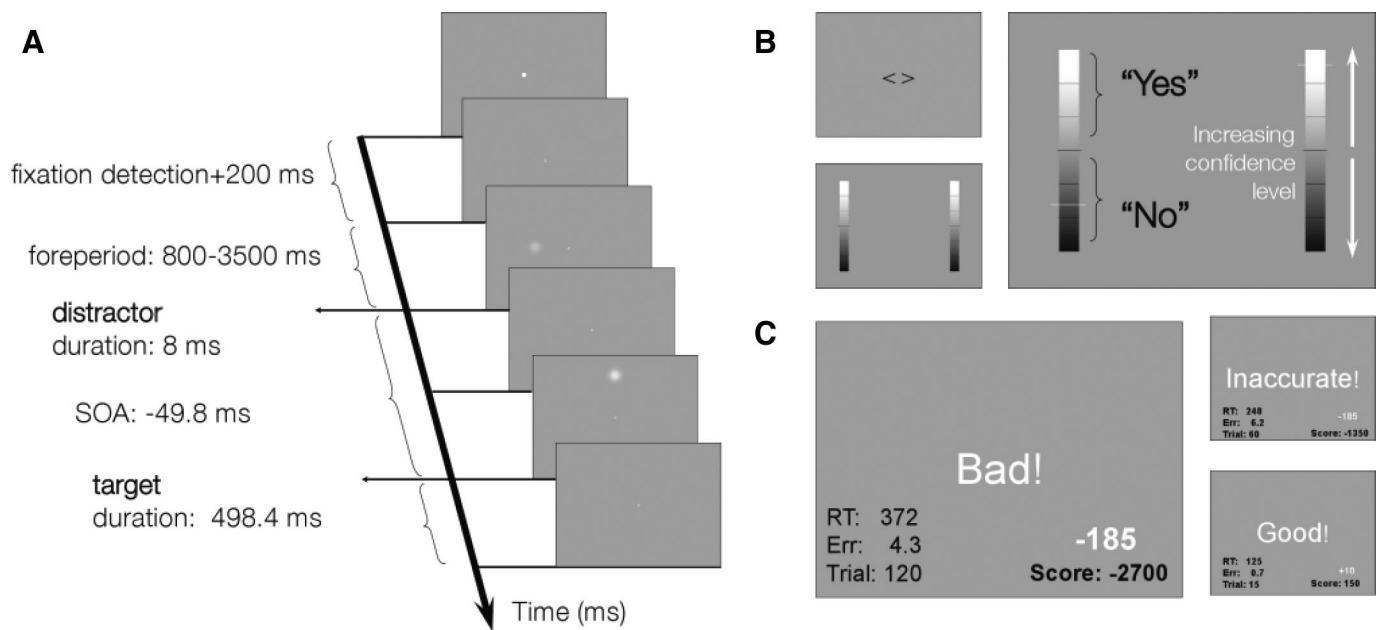


FIG. 1. *A*: 1 trial sequence illustrating the spatial and temporal configuration of the stimuli. *B*: frames presented to the participants to ask them (*top left*) to report the location of the distractor in the 2AFC experiment or (*bottom left*) to indicate for each distractor their confidence of having or not seen the distractor in the yes/no-rating experiment. This 2nd response frame is further detailed on the rightmost image. *C*: examples of feedback screens. Proportions and colors have been modified for sake of visibility of this figure.

PRELIMINARY EXPERIMENT 2: 2AFC. The aim of this experiment was to assess the contrast value that yields a detection d_a of 1 as well as observers' latencies to be used for the feedback rules in the main experiment. The distractor was presented either on the left or on the right of the fixation dot, and observers pressed the left or right mouse button to indicate (after their saccade) its location. The luminance of the distractor was modified using a Bayesian adaptive procedure¹ to estimate the contrast corresponding to 76% correct responses.²

The feedback rules in this condition differed from those in the fast saccades condition. Trials with saccade endpoint errors ($>2^\circ$) or with latencies <100 ms or longer than the 95th percentile of the fast saccades distribution were followed by a negative feedback ("anticipation", "too slow", or "inaccurate") and a 185-point loss. Correct saccades were rewarded with 15 points and a "good" message. These rules were chosen to provide an average score of 5 points per trial for an expected 5% invalid trials (as defined by the feedback rules). As observers were nonetheless unable to achieve such a low percentage

of rejected trials they almost always finished the experiment with negative scores.

This preliminary experiment consisted of 300 trials: 200 trials used by the adaptive procedure and 100 randomly interleaved no-distractor trials. The latter were used to assess each observer's latency to the target in the dual task of the main experiment. The 95th percentile of this latency distribution was used as the criterion for the latency feedback rule in the main experiment. The whole 2AFC experiment lasted ~ 35 min per participant.

MAIN EXPERIMENT: YES/NO RATING AND SACCADE. The main experiment was identical in all aspects to the 2AFC condition except for the following points. The distractor appeared with a probability of 0.5 independently on the left and on the right of fixation so that the presence/absence of one distractor was not informative as to the presence/absence of the second distractor. Thus there were 25% no-distractor trials, 25% two-distractors trials, and 50% one-distractor trials (i.e., 25% on the left and 25% on the right of fixation).

As in the preliminary experiments, participants' task was first to saccade as fast and precisely as necessary to the target stimulus. If the saccade parameters (latency or landing position) were outside the acceptable range, participants received a visual feedback and a negative score and no response relative to the presence of the distractors was requested. If their saccade was acceptable, two vertical stripes, each subdivided in six equal-sized segments appeared on both the left and the right side of the screen. Participants were to click on 2 of the 12 segments, i.e., 1 on the left, the other on the right, to indicate their confidence of having seen (3 upper segments) or not having seen (3 lower segments) the distractor on the corresponding side with confidence increasing from the central to the extreme segments (see Fig. 1*B*). Observers were asked to use as much as possible the whole range of the confidence scale with no time pressure for providing their responses. Their confidence judgments were validated only after they pressed the central button of the mouse. At that point, they received the positive feedback and score relative to their saccade. Note that in the present dual-task experimental design distractors are irrelevant to the motor task so that a putatively dissociated motor system could, in principle, ignore them. The correlation between perceptual and motor responses should argue against such dissociation. The strength of this

¹ This procedure was developed and implemented in Matlab by S. Barthelmé and P. Mamassian (unpublished data). The software can be freely downloaded at [http://sites.google.com/site/simonbarthelme/software]; for a similar procedure see Kontsevich and Tyler (1999).

² The correspondence between percentage correct in a 2AFC task and the d_a in a yes/no+rating task is given by

$$P_{correct} = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{d_a} \exp(-x^2/2) dx \quad (1)$$

With

$$d_a = \frac{\mu_S - \mu_N}{\sqrt{\frac{\sigma_S^2 + \sigma_N^2}{2}}} = \left(\frac{2}{\sigma_S^2 + \sigma_N^2} \right)^{1/2} (\mu_S - \mu_N) \quad (2)$$

where μ_S , σ_S and μ_N , σ_N , are the mean and SD of, respectively, the signal and the noise distribution (Macmillan and Creelman 2005, p. 62). This standard derivation has been recently challenged (Yeshurun et al. 2008).

logic depends, however, on the extent to which the two systems share a unique attentional system and on this latter's spatial selectivity.

The derivation of observers' receiver operating characteristic curves, ROCs, from his/her confidence settings served two purposes. First, computing d' from simple yes/no responses yields wrong perceptual sensitivity estimates when signal and noise distributions have different SDs. Second, it allows the assessment of multiple internal response levels on a continuous scale which can be used to estimate quantitatively the relationship between the internal perceptual response and the magnitude of the saccade curvature supposedly reflecting an internal "motor" response.

The main experiment consisted in 6–11 blocks of 100 trials each with 1 block lasting ~10 min. The complete experiment was passed in two different days and lasted between 2 and 3 h per participant.

Participants

Five naïve observers and the first author (4 women, 2 men—25 to 29 yr old) participated in all experiments. They had normal or corrected-to-normal vision.

Data analysis

Trials were excluded during (means \pm SE = 16.85 \pm 2.24%; see METHODS) and/or after the experiment if saccade latencies, amplitude, curvature, or landing position were without $\times 2$ the interquartile range (iqr) of their corresponding distribution. This led to an average exclusion rate of 25.62 \pm 2.75%, which is similar to what has been reported earlier (e.g., 22% in Doyle and Walker 2001). The positional data (x and y coordinates of the gaze, expressed in degrees of visual angle relative to the fixation point) were analyzed both on-line (to provide a trial-by-trial feedback) and off-line. They were filtered (forward and reverse for a zero-phase shift of the curves) using a second-order Butterworth dual-pass filter (cutoff frequency: 10 Hz). Saccades were first roughly situated within the velocity profiles with a high threshold (100 %/s) and more precisely detected by fitting (least squares) an L-shaped function (2 line segments) to the velocity profiles of the horizontal, vertical and tangential dimensions of the eye movement. This L-shaped function is defined as a constant before the moment of saccade initiation and as a linear function thereafter. The slope of this second linear function represents the initial velocity of the x , y , and tangential displacements. Saccade offsets were determined as the first velocity minimum after the tangential velocity dropped <75 %/s. The coordinates of the gaze at saccade onset and offset correspond respectively to the saccade start and end points, and the Euclidean distance between these points is the saccade amplitude. Curvature is defined as the area comprised between the straight line that relates the start and the end of the saccade and the trajectory of the saccade divided by the amplitude of the saccade (Ludwig and Gilchrist 2002). The sign of the curvature corresponds to the sign of the abscissa: right- and left-hand saccade deviations are given positive and negative signs, respectively.³ As saccade trajectories tend to be curved even in the absence of distractors (Dodge 1917), curvature is usually expressed with reference to this baseline curvature. In RESULTS in the following text, C_0 refers to the curvature difference relative to the no distractor condition (e.g., Doyle and Walker 2001) independently of participants' perceptual responses. As saccade curvatures are also to be classified according to the latter, we define a curvature change, C_{2CR} , relative to the condition where no distractors were present and observers correctly reported both of them to be absent (double CR trials).

³ Some authors defined the curvature sign to be positive when the distractor attracts the saccade trajectory, and negative in the opposite case (e.g., Doyle and Walker 2001). Obviously, when two distractors are present, these notions are ill-defined, and it is necessary to express curvature independently of the distractors (e.g., McSorley et al. 2004).

RESULTS

Perceptual responses

Perceptual sensitivity (d_a , see Eq. 2 in Footnote 1) and decision criteria (c_a) were estimated by fitting ROC functions to the cumulative conditional probabilities of observers' confidence ratings (of having seen the stimulus given the presence or absence of the signal) (Macmillan and Creelman 2005). The decision criteria for the seen/not seen responses are given by the negative z -score of FA [$c_a = -z(\text{FA})$, i.e., the "absolute" criterion] (see Gorea and Sagi 2000). Figure 2A illustrates the ROC curve of a representative subject for the right-hand distractor and B shows the underlying signal (gray) and noise (black) distributions together with the five decision criteria/confidence ratings (vertical dotted lines; the solid vertical line represents the yes/no criterion) that separate each distribution into the six confidence levels. The mean internal response associated with each confidence level is shown as a gray triangle for the signal and as a black triangle for the noise distribution, together with their corresponding SDs, represented by the horizontal error bars.⁴ Solid circles in the upper part of Fig. 2B represent the mean and SD of the internal responses corresponding to the standard correct rejection (black), miss (dark gray), false alarm (light gray), and hit (white) response categories. These internal response means and SDs will be used to assess the quantitative relationship between perceptual and motor responses (see *Curvature as a function of both left- and right-hand sided internal responses*).

The individual perceptual d_a values ranged from 0.441 to 1.775; the σ_N/σ_S values (i.e., the slopes of the ROC in z coordinates; ranged from 0.168 to 0.816. Only one of the six observers exhibited a higher d_a for the left than for the right distractor with the mean d_a for the right-hand distractor [1.172 \pm .197 (SE)] slightly higher than the mean d_a for the left-hand distractor (0.988 \pm .185). This difference was not significant [paired t -test, $t(5) = -2.256$, $P = 0.074$]. The σ_N/σ_S ratios for the two sides (right distractor: 0.496 \pm .062; left distractor: 0.471 \pm 0.089) were virtually identical [$t(5) = -0.530$, $P = 0.619$]. It should be noted that because the derived signal and noise variances were different, computing d' from the yes/no responses (instead of the ROC-based d_a) yields systematically biased sensitivity measures ($d' = 1.568 \pm .184$) with this error

⁴ The mean and SD of the internal response associated to a particular confidence level, delimited by the criteria c_1 and c_2 are given by

$$m = \frac{\int_{c_1}^{c_2} xN(x;\mu,\sigma)dx}{\int_{c_1}^{c_2} N(x;\mu,\sigma)dx} \tag{3}$$

$$s = \sqrt{v}; \quad \text{with} \quad v = \frac{\int_{c_1}^{c_2} (x - m)^2 N(x;\mu,\sigma)dx}{\int_{c_1}^{c_2} N(x;\mu,\sigma)dx} \tag{4}$$

where μ and σ are the mean and SD associated with either the signal or noise distribution and N is the normal distribution.

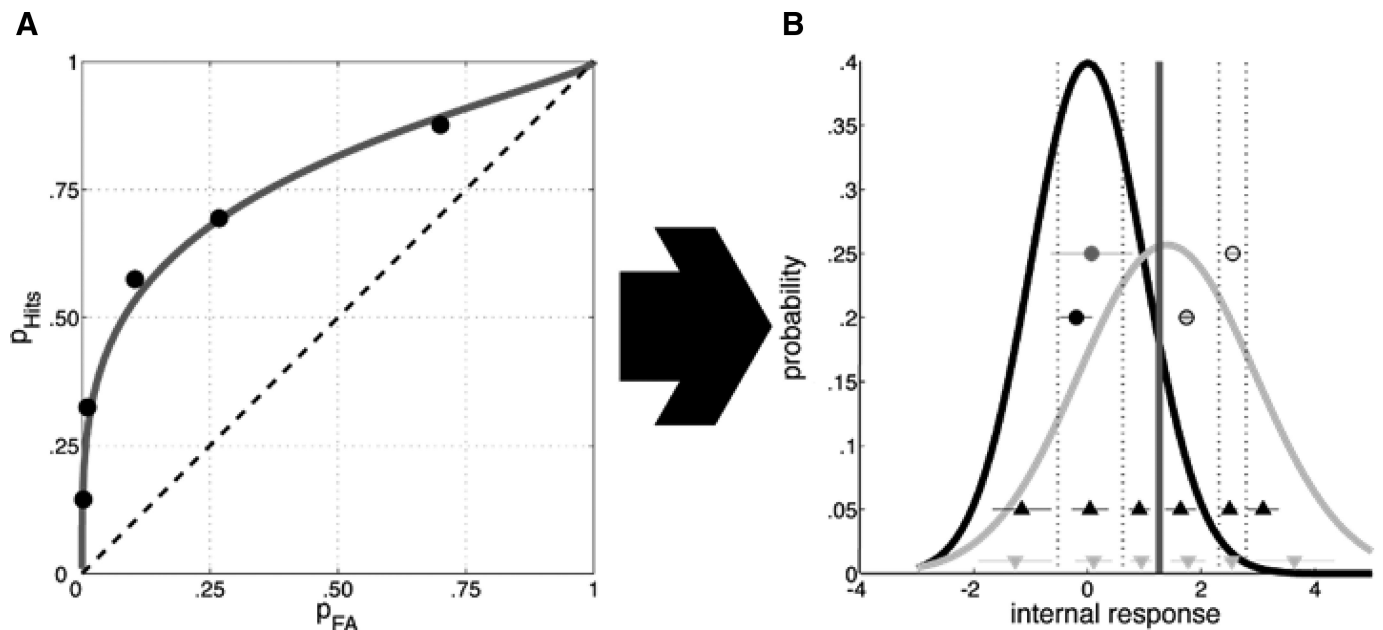


FIG. 2. *A*: receiver operating characteristic (ROC) function of 1 observer. Dots are measured false alarm (FA) and hit rate pairs for 1 distractor location conditional on a correct rejection for the other location. *B*: black and gray curves are, respectively, the noise and signal distributions derived from the ROC curve. Vertical lines represent the decision criteria separating the internal responses in the six response categories used by the observer (the solid line is the seen/not seen criterion). Triangles represent the mean internal response associated with each of these response categories (black for the noise and gray for the signal distribution) and dots represent the mean internal responses associated with correct rejections (black), misses (dark gray), FAs (light gray), and hits (white). Horizontal lines are the corresponding SDs.

being dependent on the participants' decision criteria. Assessing the ROC curves is thus imperative.

Observers' decision criteria did not depend on the distractor's location either [$t(5) = 0.011$, $P = 0.992$]. They showed no significant left-right correlation across subjects whether the criteria were computed based on all trials (Spearman $r = 0.657$, $P = 0.175$) or when excluding the two-distractors-present trials [$t(5) = 0.238$, $P = 0.821$; Spearman $r = 0.600$, $P = 0.242$]. These results indicate that observers set their left- and right-side criteria independently.

To determine whether the perception of one distractor was independent of the *presence* of the other distractor, the d_a ROC analysis above was performed separately for the left- and right-hand distractors conditional on the presence/absence of the right- and left-hand distractor, respectively. Paired t -test revealed no difference between either the d_a [$t(5) = -0.514$, $P = 0.629$] or the σ_N/σ_S ratios [$t(5) = 0.537$, $P = 0.614$] for one location depending on whether or not a distractor was present at the opposite location. Taken together, these sensitivity and signal-to-noise ratio analyses point to the fact that observers coded the left- and right-side distractors independently of each other.

In contrast, the decisional behavior for one location did depend on the presence/absence of a distractor at the opposite location [$t(5) = 2.618$, $P = 0.047$], with $c_a \sim 1.225$ times larger

(median, $iqr = 0.365$) when the opposite distractor was absent. Whether this dependence results from the use by observers of a complex decisional space or reflects a trivial bias induced by the present dual rating design remains unknown. To circumvent the potential inference of such decisional unbalanced behavior, the relevant analyses in the following text excluded the two-distractors-present trials.

Motor responses

The Jarque-Bera normality test (Jarque and Bera 1987) performed on each observer's computed raw curvature distributions showed that only for one of six participants, and only in the distractor free condition, the P value was below 0.05 ($P = 0.026$). Given the number of performed tests ($6 \times 4 = 32$), it is reasonable to conclude that the curvature is normally distributed. The mean (\pm SE) saccadic curvature, latency and landing position (across observers) are given in Table 1 for the four stimulation conditions (i.e., no distractor, distractor present on the left only, on the right only, and 2 distractors present).

Figure 3 shows the average trajectory *differences* relative to the no distractor condition, C_0 , separately for each observer (different symbols) and stimulation condition (different gray levels, filled and empty symbols). Relative to C_0 , saccades

TABLE 1. Means of saccadic curvatures, latencies, and landing positions relative to the target location (\pm standard error of across subjects mean) for the four stimulation condition used

	No Distractor	Distractor Left	Distractor Right	Two Distractors
Curvature, deg	0.154 ± 0.085	0.256 ± 0.090	0.067 ± 0.093	0.169 ± 0.103
Latency, ms	230.442 ± 16.677	230.187 ± 15.214	229.544 ± 14.557	226.753 ± 13.470
Horizontal error, deg	-0.152 ± 0.058	-0.124 ± 0.059	-0.158 ± 0.056	-0.158 ± 0.063
Vertical error, deg	-0.456 ± 0.070	-0.406 ± 0.063	-0.449 ± 0.073	-0.416 ± 0.052

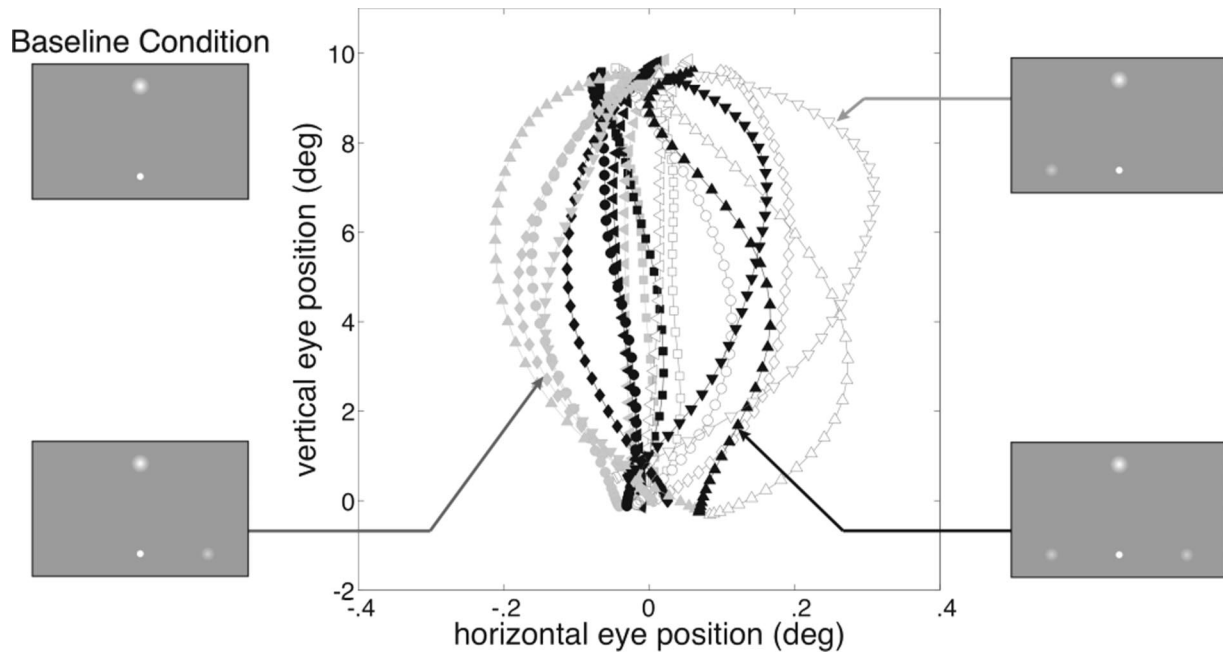


FIG. 3. Average saccade trajectory change relative to distractor absent condition C_0 . Light solid symbols and open symbols curves represent respectively the right and left distractor only conditions. Dark symbols show the 2 distractor conditions. Different symbols are for different participants.

curve to the right when the distractor is presented on the left and vice versa. The curvature effect of the left and right distractors was assessed with a three-way ANOVA [factors left distractor (present/absent), right distractor (present/absent), and participant (1–6)]. The ANOVA yielded a significant main effect of both left [$F(1,23) = 136.509$, $P < 0.001$] and right distractors [$F(1,23) = 98.789$, $P < 0.001$] indicating that their presence increased the curvature magnitude. These two factors (distractor sides) did not interact [$F(1,23) < 1$], suggesting that the effects on the curvature of one of the two distractors (presence/absence) is independent of the other distractor. Finally, there were significant between-subject differences in mean curvature [$F(5,23) = 430.053$, $P < 0.001$], most likely due, at least partly, to between-subject sensitivity differences (see *Confronting perceptual and motor responses*). We also computed for each observer the mean repulsion effect in conditions where only one distractor was present (collapsing the data across distractor locations) relative to their mean curvature in the no-distractor condition. The mean \pm SE repulsion effect was 0.189 ± 0.051 and significantly different from 0 [$t(5) = 3.730$, $P = 0.014$].

An equivalent analysis performed on saccade latencies failed to reveal a significant effect of the presence/absence of the left distractor [$F(1,23) = 3.137$, $P = 0.137$] on saccade latencies but yielded a marginally significant effect for the right distractor [$F(1,23) = 6.351$, $P = 0.053$]. Again the interaction between the distractor effects was not significant [$F(1,23) = 2.176$, $P = 0.200$], while the latency difference between participants was [$F(5,23) = 1209.803$, $P < 0.001$]. Almost identical saccade latencies for distractor-present and -absent trials suggests that the distractor was not used as a trigger signal (Doyle and Walker 2001; Ross and Ross 1980).

Finally, we performed a similar analysis on the x and y coordinates of the saccade endpoints. The presence/absence of the left distractor had no effect on the horizontal coordinate of the saccades landing points [$F(5,23) = 1.104$, $P = 0.342$] but

had a marginal effect on its vertical coordinates [$F(5,23) = 6.746$, $P = 0.048$]. The right-hand distractor had no effect on either of the x - y coordinates [horizontal: $F(5,23) = 2.326$, $P = 0.188$; vertical: $F(5,23) < 1$]. The interaction between the left and right-hand distractors was not significant for either of the x - y coordinates [horizontal: $F(5,23) = 1.131$, $P = 0.336$; vertical: $F(5,23) < 1$]. Finally, there were significant between-subject differences in mean saccade endpoints [horizontal: $F(5,23) = 79.316$, $P < 0.001$; vertical: $F(5,23) = 56.511$, $P < 0.001$].

Of the 24 Spearman rank correlations between curvature and latency computed separately for each observer and each distractor configuration (6 observers \times 4 configurations), 11 were significant, 6 of which were negative, and 5 positive. The sign of these correlations was unrelated to the distractor configuration, suggesting that, if at all, the relationship between curvature and latency is complex. The absence of a systematic latency-curvature correlation is concordant with previous studies having used, as in here, predictable distractor locations (but high contrast stimuli) (e.g., Doyle and Walker 2001; McSorley et al. 2004; Walker et al. 2006). Note that for unpredictable target and/or distractor locations, the literature agrees in that short-latency saccades curve toward the distractor, whereas long-latency saccades curve away from it (for a review, see Walker et al. 2006).

To sum up, the present results show that saccade curvature, but not latency, is significantly modulated by and away from the distractors location. Unsurprisingly, they also show an absence of correlation between curvature and latency. Hence within the present stimulation conditions, saccade curvature seems to be the only motor feature carrying distractor-related information.

Confronting perceptual and motor responses

SACCADIC d_A . As in the perceptual detection task, it is possible to compute a distractor detection sensitivity index based on the

saccadic curvature. There are multiple ways to compute such an index, some of which have been used to derive motor sensitivity from response time distributions (e.g., Reingold and Merikle 1988; Schmidt and Vorberg 2006). Here we computed a saccade curvature sensitivity index using two distinct methods. The first method, termed *effect size technique* by Schmidt and Vorberg (2006), expresses motor-sensitivity as the mean curvature difference between one- and zero-distractor conditions normalized by the square-root of the mean of their variances (trials where both distractors were present were excluded from this analysis). According to this effect size technique, perceptual and saccadic d_a (computed on the very same trials) are significantly correlated (Spearman $r = 0.943$, $P = 0.017$) with perceptual d_a systematically higher than saccadic d_a [$t(5) = 11.389$, $P < .001$] by an average of 0.771 noise units (median; iqr = 0.250).

Arguably, saccadic d_a are lower than perceptual d_a because the execution of the saccade yields additional motor noise. We hence used a second motor d_a estimation method whereby saccade curvature reflects the linear sum of a motor decisional (D) and an execution related (K) random variable. K is normally distributed and independent of the stimulation condition (i.e., its mean and variance do not depend on the presence/absence of the distractors). The decision random variable D determines the magnitude and direction of the distractor induced curvature; it can be modeled as the difference between the internal (motor) evoked responses to the left and right distractors. The distribution of the left distractor evoked internal responses in the distractor present condition is noted signal left, S_L , and the internal response distribution in its absence is noted noise-left, N_L . The equivalent S_R and S_N notations are used for the distractor present/absent cases on the right side. The observed raw curvature C is then given by the sum of five random variables each defined by two parameters, the mean \pm SD (10 parameters total)

$$C = [p_L \times S_L + (1 - p_L) \times N_L] - [p_R \times S_R + (1 - p_R) \times N_R] + K$$

with p_L and p_R equal to 1 if the left and right distractors are present and equal to 0 otherwise. Assuming that the two signal distributions, S_L and S_R , and the two noise distributions, N_L and N_R , have equal means \pm SD, C can be modeled with only six free parameters (mean \pm SD of S , N , and K), which is less than the eight parameters required to describe the data.⁵ The six fitted parameters adequately describe the present data (means; $r = 0.994$, $P < 0.001$; SDs; $r = 0.953$, $P < 0.001$). Using these fitted S and N distributions, we computed once again the saccadic d_a and compared them with the measured perceptual d_a (this time using all trials). Figure 4A shows the perceptual d_a (averaged across left and right distractor locations) as a function of the saccadic d_a derived from the linear model. The two (perceptual and saccadic) sensitivity indices were positively correlated (Spearman $r = 0.886$, $P = 0.033$) with the perceptual d_a still ~ 0.612 noise units (median; iqr = 0.317) higher than the saccadic d_a [$t(5) = 7.007$, $P < 0.001$]. Fitting the data with >6 df (i.e., allowing for the means and SDs to vary with distractor side) yielded similar results. According to this analysis, the perceptual system appears to be more sensitive than the saccadic system even when the motor-specific noise is discarded.

It should be noted that the use of the present linear model of saccade curvature distributions isolates motor sensitivity proper (derived from the S and N distributions) by partialling out the motor execution noise K . As the effect size technique does not partial out K , it necessarily underestimates motor sensitivity. The difference between the d_a s estimated with the two techniques is hence as expected.

⁵ As there were four stimulus configurations (no distractor, 1 distractor left, 1 distractor right, 2 distractors) and because the curvature distributions are normally distributed, the complete data set can be described by four Gaussian variables (i.e., 4×2 parameters), one per stimulus configuration.

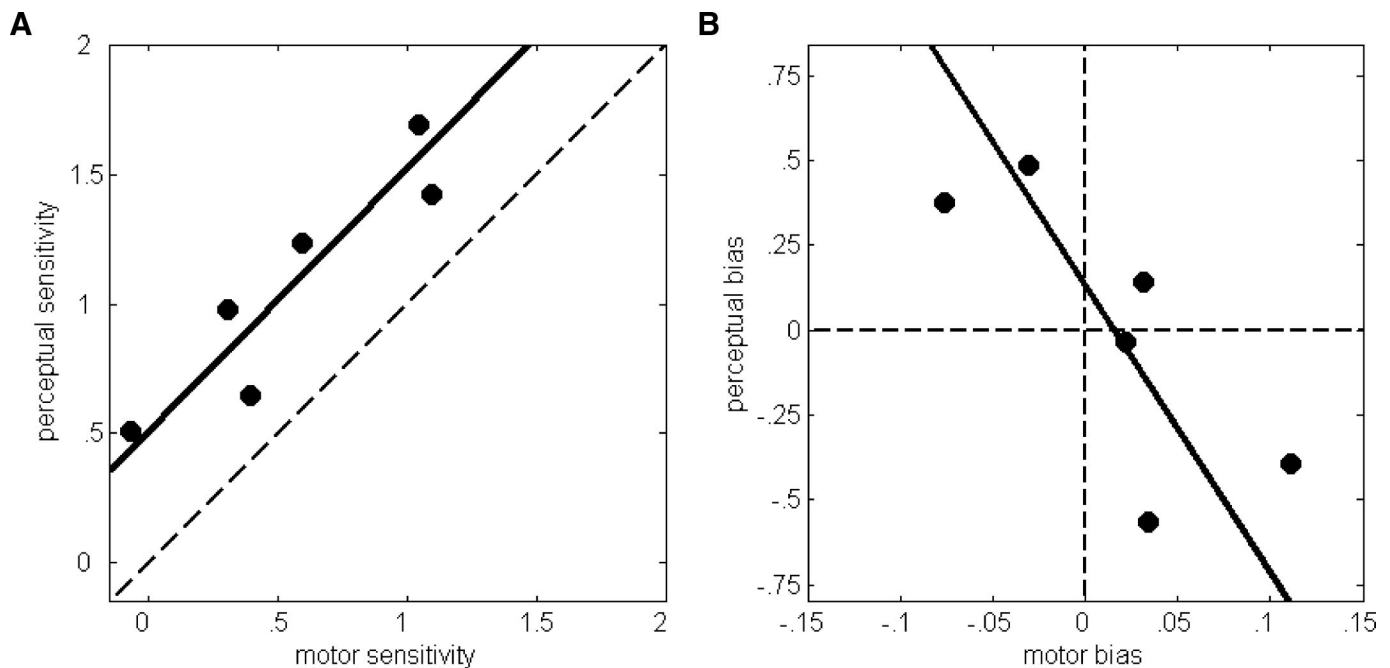


FIG. 4. A: perceptual sensitivity d_a as a function of the motor sensitivity derived from the saccade curvature distributions using a linear model (see text). B: mean perceptual bias [left-right absolute criterion difference $c_a(L) - c_a(R)$] as a function of the mean curvature difference between 2 and 0 distractor conditions, termed “motor bias” β_C . Each datum point represents 1 participant. —, least-square fits.

PERCEPTUAL AND SACCADIC BIASES. As reported in the literature (McSorley et al. 2004), the simultaneous presence of the two distractors (symmetrical about the saccadic target) entails an average (across observers) saccade curvature close to identical to the curvature assessed in the absence of distractors [$t(5) = -0.585, P = 0.584$]. This is not the case for a subject by subject analysis that reveals idiosyncratic curvature biases (β_C) for the two versus no distractors condition (C_0 ; see Fig. 3, dark curves). To determine the nature of this, presumably, motor bias, we compared β_C with the observer's absolute perceptual decision criteria, c_a (remember that there was no significant difference between the left and right c_a). This was achieved by means of computing the Spearman correlation between β_C and the left- versus right-distractor criterion differences $c_a(L) - c_a(R)$ for each observer. $c_a(L) - c_a(R)$ differences >0 indicate that for the same internal signal participants are more likely to report the presence of the right-hand stimulus (right-bias); $c_a(L) - c_a(R)$ differences <0 indicates a left-bias. If the amount of curvature depends on the perceptual decision criterion (i.e., a given "left/right" perceptual bias should entail an increased saccade curvature *away* from biased side), one should expect a *negative* correlation between perceptual [$c_a(L) - c_a(R)$] and motor (β_C) biases.

Figure 4B shows the perceptual criterion difference, $c_a(L) - c_a(R)$ ("perceptual bias") for each participant as a function of the respective motor bias. The Spearman rank correlation is negative and marginally significant ($r = -0.829, P = 0.058$), suggesting that the motor and perceptual biases are indeed related: when observers are perceptually biased to the right (reporting more liberally stimulus presence on the right), their saccades show an enhanced curvature to the left.

We reported in the preceding text a slight difference in perceptual d_a between left and right distractors. To rule out the possibility that the motor bias β_C is related to differences in sensitivity to the left and right distractors, we computed a Spearman rank correlation between the motor bias β_C and the perceptual d_a difference [i.e., $d_a(L) - d_a(R)$]. This correlation is positive but nonsignificant ($r = 0.429; P = 0.419$) thus

supporting the view that the perceptual decision criterion per se plays a crucial role in saccade curvature.

HITS VERSUS MISSES. On each individual trial, observers reported seeing or not seeing each of the two distractors. To assess the relationship between their perception of these distractors and their saccade curvature, we first analyzed only those trials where one distractor was absent and correctly reported so (i.e., CR) and the second distractor was present hence yielding both perceptual hits and misses. Figure 5A presents the mean curvature (C_{2CR}) for such hits and misses separately for the right and left distractors (error bars are 95% confidence intervals). It is clear from this figure that the curvature for miss trials does not differ from the curvature for CR trials, meaning that stimulus presence alone is not sufficient to deviate the saccades. Also apparent from this figure, the amount of curvature to the left for perceptual hits on the right-side ($0.143 \pm .039$) and to the right for perceptual hits on the left-side ($0.183 \pm .052$) are virtually identical [$t(5) = 0.971, P = 0.376$]. In the one-distractor present conditions (with the absent distractor giving rise to a CR), there was no difference in saccade latency between perceptual hits (229.305 ± 13.831) and misses [$234.206 \pm 17.751, t(5) = -0.721, P = 0.503$]. Also saccade landing x - y positions on perceptual hits ($x = -0.133 \pm .057; y = -0.396 \pm .076$) and on perceptual misses ($x = -0.1206 \pm 0.0621; y = -0.4881 \pm 0.0682$) did not differ ($x: t[5] = -0.6881, P = 0.5220; y: t[5] = 1.8243, P = 0.1277$).

Larger curvature deviations for perceptual hits than for misses are to be expected if the distractor's initial *attraction* effect is related to the perceptual response, whatever the inhibitory process applied to it at a later stage. On the other hand, a perception-independent initial attraction hypothesis predicts effects of similar magnitude for hit and Miss trials, possibly in different direction. The analysis of the curvatures for FA trials permits to narrow down the possible mechanisms subtending the present results.

FALSE ALARMS. If the saccade curvature is determined by observers' perceptual state, perceptual FAs should also curve

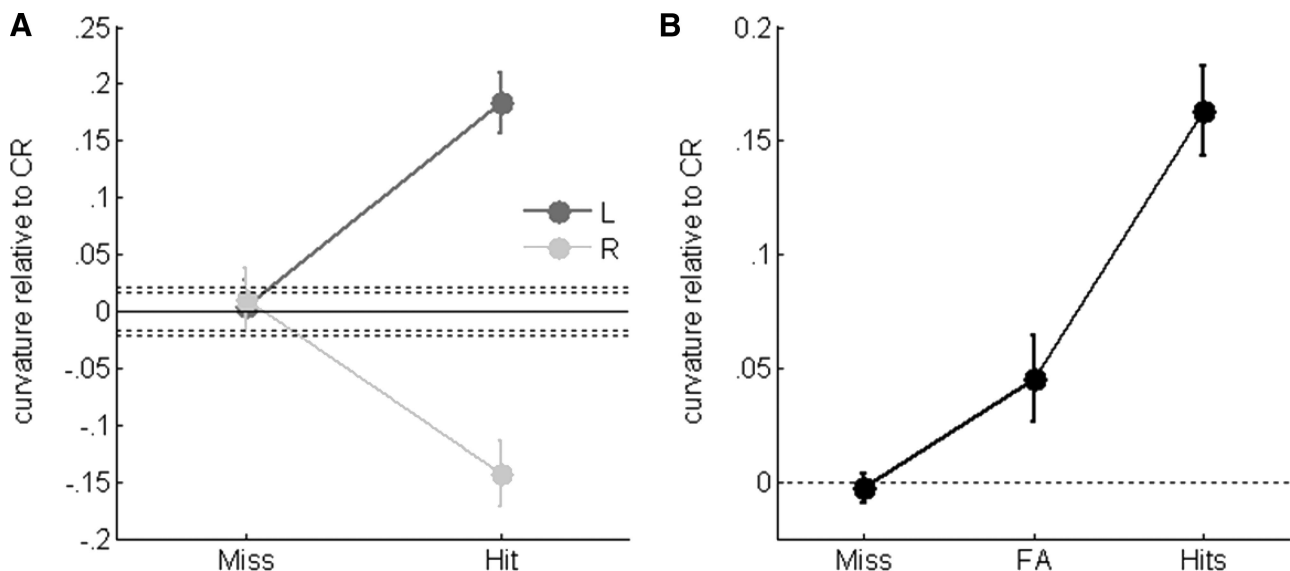


FIG. 5. A: light and dark curves represent the mean relative curvature (C_{2CR}) for perceptual misses and hits with left (dark lines and symbols)- and right-hand distractors. B: mean curvature for perceptual misses, FAs, and hits after collapsing left and right distractor conditions. Error bars are 95% confidence intervals.

saccades away from the *illusory* percept. To test this hypothesis, we included in our data those trials where no distractor was present and observers produced a FA on the left and a CR on the right or the reverse (double FAs were excluded to prevent possible confounds). As there were only very few FA and the effects of left and right distractors did not differ in magnitude, we grouped responses to left and right distractors (after changing the sign of the curvature for right distractor trials). Saccade curvatures for perceptual misses, FA, and hits are shown in Fig. 5B, with the error bars standing for the 95% confidence intervals. Clearly, saccades curve away, even from illusory percepts (i.e., FA)!

Curvature as a function of both left- and right-hand sided internal responses

In the previous analyses, we classified observers' responses as hits, misses, etc., and considered only a restricted data sample (e.g., 1 distractor condition with the absent distractor being correctly reported as being absent). This restriction was intended for clarity (see also Waszak and Gorea 2004; Waszak et al. 2007) while controlling for potential confounds. The aim of the present section is to use estimates of the mean internal responses associated with the different response confidence levels (derivable from the ROC; see Fig. 2 and Eqs. 3 and 4) to assess quantitatively the relationship between internal response and the magnitude of curvature change. In fact, as the curvature seems to be related to the perceptual criterion (rather than simply to the internal response; see PERCEPTUAL AND SACCADIC BIAS), the relationship we are looking for is between curvature change and the distance of the inferred internal response relative to the perceptual criterion c_a . Figure 6 shows the mean curvature (relative to the double correct rejection condition, C_{2CR}) as a function of the distance between the

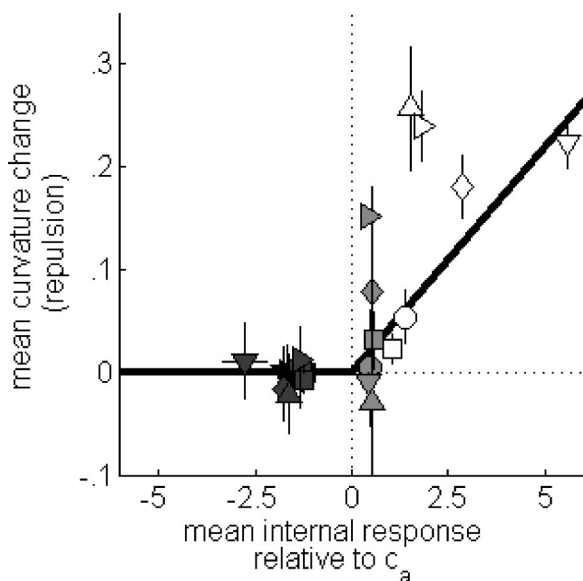


FIG. 6. Mean curvature change [relative to the double correct rejection (CR) condition, C_{2CR}] as a function of the mean internal response distance from the yes/no detection criterion c_a . Different symbols stand for different participants and different gray levels for perceptual CR (black), misses (dark gray), FA (light gray), and hits (white). Vertical and horizontal bars are ± 1 SE of the mean. The solid black curve represents the weighted total least-square fit of the mean curvatures associated with Hit and FA perceptual trials, with the inverse of the squared x - y error bars used as weights.

mean internal response associated with a given response confidence level and the absolute criterion c_a . Different symbols stand for different observers and different gray levels for perceptual CR (black), misses (dark gray), FA (light gray), and hits (white). Vertical and horizontal bars are SEs of the mean curvatures and of the derived internal responses, respectively. As the curvature effects are observed only when the internal response exceeds the absolute perceptual criterion, c_a (i.e., for hits and FA only), the average saccade curvature change on CR and miss datum points (negative x values) was set to 0 and is represented in Fig. 6 by the horizontal left-hand line. The zero intercept linear function fitted to the Hit and FA datum points (positive x values on the plot) describes the relationship between the internal response distance from the absolute criterion c_a and the magnitude of the “away” curvature change on trials where observers reported the presence of the distractor. As the datum points are noisy along both x and y dimensions, the fit was performed with a “weighted total least-squares” algorithm (Krystek and Anton 2007) where the weights associated with each datum point were the inverse of the squared SEs; these SEs are shown as horizontal and vertical error bars, respectively. This fitting procedure is such that the fitted regression line does not necessarily pass through the center of the datum points. The slope of right-hand branch is 0.044 with the 95% confidence intervals ranging from 0.032 to 0.055, indicating that a change in internal response of 1 noise unit (SD) yields a change of 0.044° in the mean curvature deviation.

The conversion of confidence response levels (1–6) into perceptual internal responses took into account the observer specific left/right sensitivities and decision criteria as well as the presence/absence of the distractors. Consequently it is possible to associate separately for each observer and for each individual trial a perceptual internal response and to quantify the trial-by-trial relationship between perceptual internal response and saccade curvature at a more general level. One way to do this is to compute separately for each observer the trial-by-trial linear partial correlations between the perceptual internal responses to a distractor and the saccade curvature while controlling for the perceptual internal responses evoked by the other distractor (this is because the curvature depends on both the left and right distractors). Across observers these partial correlations are about 0.316 (median value; iqr = 0.238) and highly significant ($P < 0.001$) for each participant, meaning that saccade curvature and perceptual response correlate on a trial-by-trial basis.

DISCUSSION

The present study investigated on a trial-by-trial basis the effects of two low-contrast distractors (presented on the left and/or the right of the fixation point) on both perceptual and motor responses. Perceptual decisions were assessed with the prototypical yes/no (distractor) detection task. Motor decisions were assessed via these distractors' effects on the trajectory of a saccade to a distinct imperative stimulus. Consequently, distractors were relevant to the perceptual but not to the motor task; in other words, perceptual and motor behaviors were not tied by a common goal.

Replicated results

The present study replicated a series of results obtained with high-contrast distractors presented at predictable spatial locations. Data show that saccades curve away from single “motor-task”-irrelevant distractors (Doyle and Walker 2001) even when they are barely visible; saccade curvature does not deviate from its baseline when the two distractors are presented at mirror symmetrical positions; presumably, distractors mutually cancel their repulsion effects (McSorley et al. 2004); and saccade latency is not affected by the distractors (McSorley et al. 2004) nor is it correlated with saccade curvature (e.g., McSorley et al. 2004; Walker et al. 2006); this suggests that, at least in the present experimental design, saccade curvature is the motor response parameter that carries the main distractor-related information. This conclusion cannot be generalized to any stimulation configuration and/or to any task constraints. The present feedback scheme and experimental design were meant to minimize latency and landing position effects to facilitate the analysis and interpretation of the curvature data. Studies having used less constrained saccadic parameters and uncertain target/distractor locations have indeed shown that, in addition to curvature, latency and landing positions also carry distractor-related information (for a recent review, see Van der Stigchel et al. 2006). To our knowledge, however, none of these studies has used near-threshold distractors.

New findings

They concern the relationship between the subjective (perceptual) reports on distractors’ visibility and saccade curvature.

CURVATURE AS A FUNCTION OF PERCEPTUAL REPORTS. It is widely accepted that motor reactions to a visual stimulus can be triggered independently of a person’s perceptual state. These motor reactions are usually assumed to rely on subcortical connections between the retina and motor-related areas (such as the superior colliculus, SC) (Perenin and Jeannerod 1975; Pöppel et al. 1973; Weiskrantz et al. 1974; for a review, see Milner and Goodale 1995). Attempts to explain why saccade trajectories are modified by the presence of irrelevant distractors posit that the mere presence of a visual stimulus evokes an activity in these subcortical maps that attracts the gaze to that location. Hence, or so the story goes, such reflexive saccades may well occur without the subject being aware of the action-triggering stimulus. It then follows that motor sensitivity should be higher than perceptual sensitivity.

To account for the finding that under some circumstances saccades deviate away from a distractor (repulsion), a number of authors postulated the existence of a second, higher-order mechanism that inhibits the distractor-related attraction and actually causes the saccade to curve in the opposite direction (Arai and Keller 2005; Godijn and Theeuwes 2002; McSorley et al. 2004; Quaia et al. 1999; Sheliga et al. 1994; Tipper et al. 2001; Walton et al. 2005). In the INTRODUCTION, we considered two possibilities concerning the interplay between the two (excitation-inhibition) processes and their dependence on observer’s perceptual state: the hypothesis that only the delayed inhibition process depends on the perceptual state with the excitation-inhibition relationship undefined and the hypothesis of a reactive inhibition process proportional to the early excitation process that precludes the possibility of one of them

being perceptual state dependent and the other not. These hypotheses generate distinct predictions as to the net saccade curvature dependency on observers’ perceptual states. The hypothesis of a perceptual state-dependent inhibition—but not excitation—predicts deviations away on hits and FA trials and deviations toward on miss trials. The reactive inhibition hypothesis predicts away saccade deviations only on hit and FA trials with no away or toward deviations on miss trials provided that the initial excitation process is perceptual state dependent; away deviations larger on signal (hits and misses) than on noise trials (FA) are predicted if the latter condition is not satisfied. In either case, the reactive inhibition hypothesis predicts no deviations toward the distractor. The present data show that saccades curve away from the distractor on both hits and FA but not on miss trials (see Figs. 3 and 5), hence supporting the hypothesis of a reactive inhibition process operating on a perceptual state-dependent excitation process. It should be noted that the absence of curvature effects on miss trials is most likely unrelated to the use of low contrast distractors in the present study. First, our distractors did entail significant saccade curvatures so that they should be regarded as relatively “strong” for the motor system. Second, in a previous experiment, we have shown that a perceptually missed prime of a given contrast affected or did not affect the motor response (simple RT) depending on whether this prime was masked or not (Waszak et al. 2007). These results suggest that stimulus contrast is not the unique factor determining “subliminal” motor effects.

As numerous studies have consistently reported that saccade trajectories deviate away from overtly or covertly *attended* spatial locations (e.g., Sheliga et al. 1994) and that attention plays a crucial role in the detection of low-contrast stimuli (e.g., Ress et al. 2000), the possibility exists that the presently observed relationship between perceptual responses and saccade curvature is mediated by a top-down (endogenous) attention process modulating both perceptual and motor behaviors. Given that the perceptual task required observers to pay attention to the two possible locations of the distractor(s), such a top-down attentional process might bind perceptual and motor behaviors only inasmuch as it displays random fluctuations across the two distractor locations. Alternatively, attention may intervene as a bottom-up (exogenous) process perceptually “grabbed” by the perturbing stimulus and subsequently triggering a motor response. Whether and how perceptual and motor responses relate to attention is a matter of future research. In the meantime, the present results show that the motor effects are contingent on the distractor-evoked internal responses that exceed the perceptual (seen/not seen) criterion.

PERCEPTUAL AND MOTOR SENSITIVITIES. The qualitative relationship between saccade curvature and observer’s perceptual state has been assessed quantitatively. In addition to deriving the standard sensitivity index (d_a) from the perceptual yes/no ROC functions, we have also inferred two motor-sensitivity indices from the distributions of saccade curvatures (see *Confronting perceptual and motor responses*). The derivation of these two indices differed in that it did or did not partial out a motor execution noise. In either case, perceptual and motor-sensitivity indices were positively correlated, with the motor-sensitivity index being 0.612 or 0.771 noise units below the perceptual index (depending on whether motor execution noise

was partialled out or not, respectively). Other studies derived motor sensitivity from the distributions of choice reaction times in a mask discrimination task depending on whether the shape of this mask was (signal trials) or was not (noise trials) congruent with the shape of a masked prime (Schmidt and Vorberg 2006; Vorberg et al. 2003). Motor sensitivity computed this way could be manipulated independently of the shape discrimination sensitivity for the masked prime (via changes of the prime-mask temporal layout). Most likely, the sensory-motor sensitivity difference also depends on the task type, that is discrimination (like in Vorberg et al. 2003) or detection (like in the present study). The fact remains that the presently observed perceptual-motor sensitivity difference could depend on the index used to derive motor sensitivity. There is no guarantee that saccade curvature captures all the information available to the motor system. Aside from saccade latencies and landing positions that in the present study were not affected by the distractor's presence, other saccade parameters such as saccade acceleration/deceleration or maximum speed) might also encapsulate motor sensitivity related information [see for example Knill and Kersten (2004), who derived a motor-sensitivity index from a linear discriminant analysis of the time course of hand movements in 3-dimensional space]. Testing the relevance of such putative motor-sensitivity indices and of their combinations is nonetheless pointless without a comprehensive model of saccades generation.

It should be finally noted that a higher perceptual than motor-sensitivity index is to be expected if the signal-to-noise ratio of the internal response increases with time (as implied by the speed-accuracy tradeoff) (e.g., Palmer et al. 2005) and if the perceptual decision is taken after the motor decision.

PERCEPTUAL INTERNAL RESPONSE AND SACCADE CURVATURE. The ROC analysis performed on the perceptual responses permitted the estimation of a mean internal response associated with a given perceptual confidence level. Our analysis took into account both between-subjects sensitivity and criterion differences as well as the physical presence of the distractors. To quantify the strength of the perceptual-motor relationship, we computed trial-by-trial correlations between the inferred mean internal response evoked by one of the two distractors and the saccade curvature while partialling out the mean internal response evoked by the other distractor. These partial correlations were about 0.316 and highly significant for each participant, implying a strong association between perceptual and motor responses. The inferred perceptually evoked internal responses exceeding the perceptual criterion were monotonically related to saccade curvature with a change in internal response of 1 internal noise unit (SD) being associated with a 0.044° change in saccade curvature away from the distractor location (Fig. 6). Other studies have also assessed the relationship between perceptual and motor responses on a trial-by-trial basis. They used a number of motor and perceptual tasks such as: the direction of smooth pursuit eye movements and the perceptual judgments of the direction of the pursued stimulus (Stone and Krauzlis 2003); pursuit speed and perceived speed (Gegenfurtner et al. 2003); simple reaction times and perceived temporal order (Cardoso-Leite et al. 2007); simple reaction times and contrast sensitivity (Waszak and Gorea 2004; Waszak et al. 2007); manual pointing and localization judgment (Gegenfurtner and Franz 2007). Except for one such

study (Gegenfurtner et al. 2003)—the conclusions of which have been questioned by Osborne et al. (2005)—all have reported significant perceptual-motor correlations. What's more, these correlations were in the same order of magnitude as the one presently assessed [e.g., 0.28 in Gegenfurtner and Franz (2007) vs. 0.32 in the present study]. This consistency, despite the large differences between the experimental paradigms, suggests that the sharing of a common substrate by perception and action may be a general principle of the sensorimotor function (Gegenfurtner and Franz 2007).

The present results show that saccade curvature correlates with observers' perceptual biases. When the two distractors were simultaneously presented at mirror symmetrical positions around the fixation point, saccades were, on average, straight although observers exhibited idiosyncratic biases to the left or to the right distractor. The tested relationship between these idiosyncratic motor biases, on the one hand, and subjects' sensitivity and perceptual criterion (left/right) asymmetries, on the other hand, showed that the motor bias correlates with the perceptual bias but not with the sensitivity asymmetry: observers that reported more frequently a distractor on a given side also exhibited saccades that curved away from that side. Variations of the perceptual bias have been observed in a previous neurophysiological study investigating the effects of temporary localized SC inactivations on monkeys' performance in a contrast detection task (McPeck and Keller 2004). Its results show that such inactivations do not affect sensitivity but significantly modulate monkeys' decision criteria: monkeys reported distractor's presence less frequently (i.e., increased their perceptual criteria). Interestingly, microstimulations of the FEF induce a significant sensitivity increase in a yes/no contrast decrement detection task (Moore and Armstrong 2003; Moore and Fallah 2001, 2004) but does not alter the decision criterion (Moore and Fallah 2004). The presently observed relationship between perceptual and oculomotor biases might thus be instantiated in the SC although it is unclear whether perceptual and/or motor decisions are actually made in the SC or forced on the SC by other areas.

In short, the present data consistently point to the conclusion that perceptual and motor responses are intimately related. Across observers perceptual and motor sensitivities and biases were significantly correlated. Within observers perceptual and motor responses correlated on a trial-by-trial basis. Saccades curved away only when observers reported the presence of the low-contrast distractors, which is to say that phenomenal experience is a necessary and sufficient condition for perturbing motor behavior. This is supported by the observation that the inferred perceptually related internal response and the curvature magnitude correlate provided that the former exceed the perceptual decision criterion.

The presently evidenced perception-action relationship may not come as a surprise even for the defendants of the strong sensorimotor dissociation view as the two behaviors are by necessity based on a common processing stream at least up to V2 (e.g., Sincich and Horton 2007). As a consequence, any early fluctuations of the incoming signal are bound to carry over to later processing stages. It remains that not all studies having compared perceptual and motor responses found their trial-by-trial correlation (e.g., Gegenfurtner et al. 2003).

Claims of a lack of perception-action correlation come from a large body of psychophysical studies having shown that the

motor system may react even to stimuli that are undetected by the perceptual system (for reviews, see Neumann 1982; Neumann and Klotz 1994; Schmidt and Vorberg 2006). Most of these studies have used a backward masking (including meta-contrast) technique and assessed observer's reaction time to (a specific feature of) the mask as a function of its shape congruence with and/or the detectability of the masked (or prime) stimulus (e.g., Klotz and Neumann 1999; Schmidt 2002; Vorberg et al. 2003). The general finding was that despite not being able to either specify the prime's shape or even detect it, reaction time to the mask was modulated by the prime's *physical* shape/presence. Many of these studies present methodological problems potentially responsible for the obtained dissociation results (see Holender and Duscherer 2004; Reingold and Merikle 1988, 1990; Schmidt and Vorberg 2006). Such criticisms aside, Waszak et al. (2007) have recently argued that at least some of the results supporting the perception-action dissociation can be accounted for by a "nondissociation" (i.e., 1 processing stream) signal detection model. Their proposal is that perceptual and motor behaviors rely on the same internal response but depend on distinct, task-dependent criteria the relative values of which will or will not entail "dissociation"-type results. One-stream two-decisions models (e.g., Ejima and Ohtani 1987; Miller and Schwarz 2006; Sternberg and Knoll 1973) have been shown to account for a number of perceptual-motor comparisons (see Cardoso-Leite et al. 2007, 2009).

Models of saccade deviation away and their neural underpinnings

Most trajectory models assume that the initial saccade direction is determined by the weighted average of the population activity in the SC the neurons of which (like those in FEF) code for a saccade to a particular spatial location (McIlwain 1991). This and other structures involved in saccade generation are not, however, exclusively devoted to the execution of a saccade. For example, SC codes for a combination of eye and head movements (Freedman and Sparks 1997; Freedman et al. 1996). Local inactivations in the SC that do not affect saccade generation can modify monkeys' decisions (McPeck and Keller 2004). Weak electrical stimulations of the FEF enhance the visually evoked responses in V4 and the contrast detection sensitivity (Moore and Armstrong 2003; Moore and Fallah 2001, 2004).

The mutually excitatory and inhibitory lateral interactions between, respectively, proximal and more distant neurons within the SC is one of the hypothesized physiological mechanisms of target selection and of the initial saccade direction (Munoz and Istvan 1998). It presumably participates in resolving the competition between target- and distractor-related activity by decreasing the latter, which causes saccades to curve toward the distractor location (McPeck et al. 2003). It has been argued that lateral inhibition can also account for the global effect phenomenon where allegedly overlapping neural activities evoked by distinct stimuli are averaged. Deviations away from a distracting stimulus require an additional, presumably inhibitory mechanism (Arai and Keller 2005; Godijn and Theeuwes 2002; McSorley et al. 2004; Quaia et al. 1999; Sheliga et al. 1994; Tipper et al. 2001; Walton et al. 2005). This inhibitory process must be contingent on subject's know-

ing which of N stimuli is/are the distractor(s). As such it must be a top-down process. In the present case where the positions of both the imperative stimulus and the distractors were known in advance, this top-down process needs not be activated on a trial-by-trial basis. Instead it may consist in a sustained inhibitory signal resulting from a motor or an attentional set established during the experimental sessions. To account for the presently observed results, such an attentional set should nonetheless randomly fluctuate across trials and the two distractor locations presently used. If so, it should also account for the presently observed absence of correlation between curvature and latency (see Walker et al. 2006).

Some authors suggested that the inhibitory signal comes from FEF (e.g., Godijn and Theeuwes 2002; McSorley et al. 2004) as this structure is known to send inhibitory connections to the SC (e.g., Basso and Wurtz 1997). Curvature away from a distractor is correlated with the decrease in the firing rate of FEF neurons coding for that distractor location (McPeck 2006) as well as with the localized inactivation of the SC (Aizawa and Wurtz 1998). That FEF may mediate top-down control is supported by this structure having reciprocal connections with extrastriate visual areas in both the dorsal and ventral streams (e.g., Baizer et al. 1991; Schall et al. 1995). It remains that no such FEF inhibitory mechanism has been positively shown to cause saccade curvature (Van der Stigchel et al. 2006).

Saccade trajectory models also assume that the final part of the saccade course (that brings the gaze back to the desired target location) is controlled by yet another structure—presumably the cerebellum (Quaia et al. 1998). Indeed the SC does not display the activation required to correct the final part of the saccade trajectory (Port and Wurtz 2003). Like the SC, the cerebellum presumably receives the spatial coordinates of the saccade goal but, unlike the SC, its activity is not affected by distractors.⁶

Although the combination of lateral interactions and top-down-inhibition can account for saccade curvature away effects, it generates numerous questions. How can lateral interactions, based on local saliency, or top-down inhibition determine which activation is related to the distractor? If such top-down inhibition exists, what is SC good for? If it is possible to generate a goal related activity that is not affected by distractors (supposedly transmitted to the cerebellum), why can't this activity also be used for the initial saccade direction? If the top-down inhibition causes saccades to curve away, why is it needed at all given that saccades ultimately land on the target, a cerebellum related achievement?

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⁶ Note that in a case like the global effect, the hypothetical distractor-independent signal sent to the cerebellum would either be affected by the distractor or not sent at all, as in such cases saccades do not land on the target location.

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