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Dynamics of distributed 1D and 2D motion representations for short-latency ocular following

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Abstract

Integrating information is essential to measure the physical 2D motion of a surface from both ambiguous local 1D motion of its elongated edges and non-ambiguous 2D motion of its features such as corners or texture elements. The dynamics of this motion integration shows a complex time course as read from tracking eye movements: first, local 1D motion signals are extracted and pooled to initiate ocular responses, then 2D motion signals are integrated to adjust the tracking direction until it matches the surface motion direction. The nature of these 1D and 2D motion computations are still unclear. One hypothesis is that their different dynamics may be explained from different contrast sensitivities. To test this, we measured contrast–response functions of early, 1D-driven and late, 2D-driven components of ocular following responses to different motion stimuli: gratings, plaids and barberpoles. We found that contrast dynamics of 1D-driven responses are nearly identical across the different stimuli. On the contrary, late 2D-driven components with either plaids or barberpoles have similar latencies but different contrast dynamics. Temporal dynamics of both 1D- and 2D-driven responses demonstrates that the different contrast gains are set very early during the response time course. Running a Bayesian model of motion integration, we show that a large family of contrast–response functions can be predicted from the probability distributions of 1D and 2D motion signals for each stimulus and by the shape of the prior distribution. However, the pure delay (i.e. largely independent upon contrast) observed between 1D- and 2D-motion supports the fact that 1D and 2D probability distributions are computed independently. This two-pathway Bayesian model supports the idea that 1D and 2D mechanisms represent edges and features motion in parallel. © 2007 Elsevier Ltd. All rights reserved.

Keywords: Contrast; Motion integration; Tracking eye movements; Bayesian model

1. Introduction

Motion processing is an essential piece of the complex visual machinery involved in the control of our actions. For instance, a brief and unexpected translation of a large visual scene elicits machine-like ocular following responses at ultra-short latencies in both humans (\sim 85 ms) and monkeys (\sim 55 ms). The initial, open-loop part of these reflexive eye movements demonstrates many of the properties attributed to low-level motion processing (see Masson, 2004; Miles, 1998 for reviews). Noteworthy, the earliest phase of the ocular following shows direction reversal with

reversed-phi motion, a phenomenon usually attributed to linear motion computation from local spatio-temporal changes in luminance (Masson, Yang, & Miles, 2002; Sheliga, Chen, FitzGibbon, & Miles, 2005). Tracking initiation is also driven by the vector average of luminance component motions in Type I plaids or patterns made of multiple Gabor patches with different carrier drifting directions (Masson, 2004; Masson & Castet, 2002). Altogether, these results suggest that the very earliest phase of reflexive tracking initiation relies on a linear motion detection mechanism followed by a rapid linear integration stage that pools luminance-based motion signals over a large, central part of the visual field (Barthélemy, Vanzetta, & Masson, 2006).

However, human ocular following responses to 2D motion stimuli such as barberpoles (Masson, Rybarzyck,

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Castet, & Mestre, 2000) or unikinetic plaids (Masson & Castet, 2002) have a more complex behavior where two independent components having different temporal dynamics have been identified: the early component (latency \sim 85 ms) drives the gaze in the direction of the component grating (1D) motion while, a later component with a latency ~ 105 ms rotates the tracking direction towards the global, 2D motion direction of the pattern. This late component seems to depend on 2D local motion cues such as line-endings in barberpoles and blobs in unikinetic plaids: affecting one or the other specifically changes the late component but leaves intact the early component (Masson & Castet, 2002; Masson et al., 2000). This complex dynamics of tracking eye movements is reminiscent of earlier psychophysical findings that, at short stimulus duration, 2D motion direction perception is strongly biased towards component motions (or a linear combinations of them) while with long stimulus durations, subjects report accurately the global 2D pattern motion direction (e.g. Lorenceau, Shiffrar, Wells, & Castet, 1993; Yo & Wilson, 1992).

Several recent studies have found similar neuronal dynamics at the level of macaque medio-temporal (MT) area. With barberpole motions, direction selectivity of MT neurons evolves over time from grating- to global motion-driven responses (Pack, Gartland, & Born, 2004). Similarly, characteristics of pattern selective cells gradually emerge over ~ 150 ms after plaid motion onset (Pack & Born, 2001; Smith, Majaj, & Movshon, 2005). The mechanism underlying this neural dynamics is still unclear. A key point is the role of the specific 2D features present in the images and whose motion in unambiguous. Several authors have suggested that localized 2D features may be extracted by some specific and delayed detectors such as end-stopped cells (Lorenceau et al., 1993; Pack, Livingstone, Duffy, & Born, 2003; Power & Moulden, 1992). Others have stressed the fact that 2D features contain high spatial frequencies that are processed by a different subpopulation of neurons (Majaj, Smith, Kohn, Bair, & Movshon, 2002). Both mechanisms postulate a specific reduction of 2D features contribution at very low contrast because both end-stopping and high spatial frequency channels vanish in this range (Derrington & Lennie, 1984; Sceniak, Ringach, Hawken, & Shapley, 1999).

Following this latter hypothesis, ones might conclude that the observed latency differences between 1D- and 2D-driven responses would be explained by the different contrast sensitivities of the neuronal mechanisms extracting local 1D and 2D motion cues. Therefore, a critical question is to understand the role of contrast gain control mechanisms in 2D motion integration (Rust, Mante, Simoncelli, & Movshon, 2006). In the context of tracking eye movements, a first goal of this study was to record ocular following in humans using single gratings, Type II plaids or barberpoles at different total contrast levels in order to probe both the contrast–response functions of early and late tracking components and the relationships between their latencies and contrast. We thus give a complete, functional description of the gain control mechanisms underlying the initiation of tracking eve movements (see also Barthélemy et al., 2006; Masson & Castet, 2002; Sheliga et al., 2005 for single 1D motions). Albrecht and coworkers have brought a large bulk of evidence for a cortical gain control mechanism that set both dynamical range and temporal dynamics of monkeys' V1 neurons (see Albrecht, Geisler, & Crane, 2004, for a review). They found that a single functional model (the Naka-Rushton equation, see Naka & Rushton, 1966) could be used to fully describe the relationships between both response amplitude or latency and contrast (Albrecht & Hamilton, 1982; Albrecht & Geisler, 1991; Albrecht, Geisler, Frazor, & Crane, 2002). A similar formalism have been used to model neuronal responses at different stages of the monkey geniculocortical pathways (e.g. Kohn & Movshon, 2003; Sclar, Maunsell, & Lennie, 1990) as well as for contrast-response functions measured at both human psychophysical (Hood, Ilves, Maurer, Wandell, & Buckingham, 1978) and behavioral (Masson & Castet, 2002; Sheliga et al., 2005) levels. Herein, we show that this functional description accounts for most of the behavioral data (e.g. response latency and amplitude) obtained for both 1D and 2D motion stimuli, so that contrast gains of 1D and 2D mechanisms can be compared. We demonstrate that such formalism is equivalent to the quadratic approximation of the probabilistic representations of the different cue velocities, as computed in a Bayesian model of motion integration (Weiss, Simocelli, & Adelson, 2002). Still, the latency differences found between 1D and 2D signals remained fairly constant across contrast range and types of 2D motion. We conclude that this latency difference cannot be explained by differences in distributed velocity representations. We must therefore postulate the existence of a pure delay within the mechanism of 2D cues computation, such as found for end-stopping in macaque area V1 (Pack et al., 2003).

2. Materials and methods

Most of the techniques have been described elsewhere (Masson & Castet, 2002) and will be only briefly summarized thereafter. Three subjects (one author and two naives) participated to this study. They were all free of neurological or eye diseases and had normal, or corrected to normal, acuity.

Visual stimuli were generated on an Sgi Octane workstation using the HIPS library (Landy, Cohen, & Sperling, 1984). All stimuli were 24 frames movies loaded into memory before the beginning of a session and back-projected on a translucent screen covering $80^{\circ} \times 80^{\circ}$ of visual field of the subject at a distance of 1 m using a video projector (resolution: 1280×1024 pixels at 76 Hz). In the first experiment, stimuli were type II "unikinetic" plaids made by adding two sine wave gratings of same spatial frequency (0.27 cpd): a dynamic vertical grating (temporal frequency: 9.5 Hz) drifting either leftward or rightward, and a static oblique grating (i.e. $\pm 45^{\circ}$ relative to horizontal). All stimuli were presented behind a circular window of 20° diameter. In the second experiment, stimuli used were barber poles made with the same sine wave vertical grating moving left/rightward but now presented behind an oblique ($\pm 45^{\circ}$ relative to horizontal) aperture with an aspect ratio of 3. To reduce the total number of conditions, we restricted grating motion directions along the horizontal axis.

Using two different orientations for both barber pole aperture and static component of uniknetic plaids made that both 1D and 2D motion directions were unpredictable. It shall be noticed however that our previous works have shown that similar temporal dynamics are observed when rotating both grating and pattern motion directions by 90° (barber pole, Masson et al., 2000; unikinetic plaids, Masson & Castet, 2002).

With both plaids and barberpoles, 1D (grating) motion directions were purely horizontal while 2D (surface) motion directions were oblique and could therefore be isolated from the vertical eye movements. In both experiments pattern motion stimuli were interleaved with single vertical gratings presented alone behind a 20° diameter circular aperture. Michelson contrast of the three different motion stimuli was systematically varied from 2.5% to 100%. Mean luminance of both the motion stimulus and the gray background was kept constant to ~22 cd/m². Display was gamma calibrated by means of a lookup table.

The behavioral paradigm has been described previously (Gellman, Carl, & Miles, 1990; Masson et al., 2000; Miles, Kawano, & Optican, 1986). Trials started with mean gray screen and a red target was back-projected at 10° to the right of the center using a laser diode. Once subject has fixated this target for 500 ± 200 ms, it was turned off and replaced by a central target that the subject was instructed to capture with an accurate and brisk saccade. During the saccadic flight, central fixation point was extinguished. Motion stimulus was presented shortly (~50 ms) after the end of the saccade, with total stimulus duration of 200 ms, after which the screen was blanked, ending the trial. Stimuli presentation order was randomized and interleaved with a catch-trial where motion stimulus was replaced by a grey screen. For each subject, we collected ~150 trials

per condition, in several (\sim 30) daily recording sessions. Horizontal and vertical positions of the right eye were recorded using the scleral search coil technique (Collewijn, van der Mark, & Jansen, 1985; Robinson, 1963). Online control of behavior, stimulus control and data acquisition (sampling rate: 1 KHz) was done using the REX package (Hays, Richmond, & Optican, 1982).

Eve position data were linearised, filtered using a spline procedure (Busettini, Miles, & Schwartz, 2001) to remove high frequency noise and differentiated to compute horizontal and vertical eye velocity profiles. We report the effects of stimulus contrast upon ocular responses in two different ways. By plotting the mean (across trial) eye velocity profiles we illustrate the full dynamics of ocular tracking responses (e.g. Fig. 1a). To give quantitative estimates of the input-output transfer function, we computed changes in both horizontal (Δe_h) and vertical (Δe_v) eye position over four different time windows, lasting 20 ms and starting at 95, 115, 135 and 155 ms after stimulus onset. Thus, the latest time window (155-175 ms) was still in the open-loop period of both late and early response components. We plotted the mean (\pm SE across trials) amplitude against contrast, for each subject and 1D/2D motion direction (e.g. Fig. 1c). Mean $(\pm SD)$ changes in horizontal and (corrected) vertical positions were computed across the different motion direction conditions after proper rotation.

To isolate the relationship between contrast and either 1D or 2D response components, we had to correct eye movement recordings from two potential artifacts. First, horizontal and/or vertical ocular responses to motion stimuli might have been contaminated by residual eye velocity drift due to the centering saccades. We applied the same procedure as



Fig. 1. Contrast–response function for single grating motion. (a) Mean ($n \ge 120$) horizontal eye velocity profiles of ocular responses to a leftward grating motion, presented at different contrasts, as indicated by numbers at the right-end of the curves. The gray bar illustrates the first time window (95–115 ms) used to compute the earliest change in eye position. (b) Mean (\pm SD) latency of ocular responses, as a function of grating contrast. Continuous line is the best-fit inverted Naka–Rushton function. (c) Mean (\pm SD) amplitude of the earliest ocular responses, as a function of grating contrast. Continuous line plots the best-fit Naka–Rushton function. (d) Best-fit contrast–response functions obtained for each temporal window. The inset shows, for each subject, the time course of mean half-saturation contrast.

developed by Miles and colleagues (see Busettini et al., 2001) to remove this component from the stimulus-driven responses. For each condition, we subtracted the mean eye velocity profiles and mean $\Delta e_{\rm h}$ or $\Delta e_{\rm v}$ obtained with the catch-trial condition from those obtained with moving stimuli. Second, we corrected for any misalignment between eye coil and visual screen coordinate systems or other caveats that can result in a small but significant cross-talk between horizontal and vertical eye movements, at least in some subjects. Our strategy to disentangle grating- and patternrelated response components is to project them onto horizontal and vertical axis of eye movements. Therefore the vertical eye movements must be free of any slow drifts due to some unspecific vertical responses that could be observed even when presented with pure horizontal motions of a single grating. To eliminate these spurious responses, we processed both mean vertical eye velocity profiles and mean $\Delta e_{\rm v}$ in the following way. The mean vertical responses obtained for a given contrast value of the single grating motion conditions were subtracted from the corresponding mean vertical responses obtained with a moving barberpole or plaid motion at the same contrast level. Therefore, vertical eye velocity profiles illustrated in Figs. 2 and 4 are corrected responses. Mean vertical response amplitudes plotted in Figs. 2b, 3, 4b and 5 are corrected responses that reflect the pure relationship between contrast and 2D-driven responses. All subsequent analyses (i.e. fitting curves or computing mean and normalized response amplitudes) were done using these corrected vertical responses.

Relationships between ocular response amplitude and contrast were measured for each subject and for both grating (i.e. early component) and global (i.e. late component) motion direction. Individual and mean data across conditions where fitted with a Naka–Rushton function (Naka & Rushton, 1966) of the following formula:



Fig. 2. Contrast–response functions for unikinetic plaids. (a) Vertical and horizontal mean velocity profiles of ocular responses to unikinetic plaids of different contrast. Grating motion direction is leftward and plaid motion direction is leftward and upward. The gray bars illustrate the two time windows (95–115 and 115–135 ms) over which changes in horizontal and vertical eye positions are computed, respectively. (b) Mean (\pm SD) amplitudes of horizontal (open symbols) and vertical (closed symbols) ocular responses to plaid motions, plotted against plaid contrast. Continuous lines are best-fit Naka–Rushton functions. Subject G.M.



Fig. 3. Temporal dynamics of contrast–response functions for unikinetic plaids. From left to right are presented the relationships between horizontal (open symbols) and vertical (closed symbols) change in eye position and plaid contrast, for each subject and for three pairs of time slices. For each time slice, the time windows for measuring vertical response component are shifted by 20 ms relative to those for horizontal response component to illustrate similar response time epoch of the late and early component, respectively.



Fig. 4. Contrast–response functions for barberpole motions. (a) Vertical and horizontal mean velocity profiles of ocular responses to barberpoles of different contrast. Grating motion direction is leftward and barberpole motion direction is leftward and upward. Grey bars illustrate the two time windows, as in Fig. 2a. (b) Mean (\pm SD across directions) amplitude of horizontal (open symbols) and vertical (closed symbols) ocular responses, plotted against barberpole contrast. Continuous lines are best-fit Naka–Rushton functions. Subject G.M.



Fig. 5. Temporal dynamics of contrast-response functions for unikinetic plaids. Same plots as in Fig. 3, for barberpole motion. Open and closed symbols represent changes in horizontal and vertical positions, respectively. The same pairs of time windows are used as in Fig. 3.

$$R_{\rm c} = R_{\rm max} \left[\frac{c^n}{c^n + C_{50}^n} \right]$$

From this fit, we can estimate the contrast at the half-maximum response amplitude (C_{50}) and the exponent (*n*) of the contrast–response functions of both 1D- and 2D-driven tracking components. Quality of each fit was assessed by computing its normalized χ^2 value. Fits were computed for each set of mean changes in eye positions obtained for a given motion direction. The statistical significance of the difference between 1D and 2D fitted parameters was tested with a Friedman's nonparametric two-way ANO-VA with two factors (motion direction and 1D/2D cues) (Hollander & Wolfe, 1973). We found no significant effects of motion direction for all parameters. Therefore, we computed mean amplitude across motion directions and fit these results with the same function. Fittings contrast–response functions from changes in position averaged either across trials or direction gave identical results, so this is the best-fit curve obtained by using the mean changes in amplitude across motion directions, which are illustrated in Figs. 1-5 and 7.

Differences in response amplitude do not necessarily reflect only the differences in the visual processing for different contrasts, because of anisotropies within the oculomotor system. Therefore, we performed the same analysis after normalizing changes in position data between 0 and 1, across the whole contrast range of a given condition, by mean of the following formula:

$$R_{\rm norm} = 1 - \frac{R_{\rm max} - R_{\rm c}}{R_{\rm max} - R_{\rm min}}$$

where $R_{c,} R_{max}$, and R_{min} are mean changes in position of responses observed for a given contrast, for the largest and for the smallest responses over the full range of contrast, respectively. Objective estimates of the

latencies for early and late responses components were computed for each subject and for each grating and pattern direction conditions by mean of an objective method, which has been described earlier (Krauzlis & Miles, 1996; Masson & Castet, 2002). The relationship between mean latency (across motion directions) and contrast were fitted with an inverted Naka–Rushton equation, which has the following formula:

$$\tau_{\rm c}(c) = \tau_{\rm max} + \tau_{\rm shift} \cdot \left[\frac{c^n}{c^n + S_{50}^n}\right]$$

where τ_{max} and τ_{shift} are the minimum latency observed at the highest contrast and the maximum decrease in latency, respectively. *n* is the latency shift exponent, S_{50} is the latency shift half-saturation and *c* is contrast. Both Naka–Rushton and inverted Naka–Rushton functions were fit using the Nelder–Mead simplex algorithm (Matlab[®]).We used a similar procedure to fit our model to the experimental data and compare the quality of fits with those produced by applying the model of Weiss et al. (2002). The χ^2 value was minimized by the fitting procedure

3. Results

We ran two successive experiments. In the first experiment, plaids and single gratings were interleaved. In the second experiment, we presented the same drifting gratings behind either a circular window or an elongated rectangular aperture, the later forming a barberpole motion stimulus with an aspect ratio of 3. Because grating motion conditions from each experiment gave identical ocular following responses, we will first report the contrast dependency of earliest ocular following to grating motion alone by averaging the two data sets.

3.1. Ocular responses to single grating motion

Fig. 1a illustrates the horizontal eye velocity profiles for one subject in response to a leftward drifting grating presented at different contrast levels. Increasing contrast resulted in a shortening of response latency and a brisk increase in initial eye velocity. Latency reduction rapidly saturated as shown by the overlapping eye velocity onsets for contrast above 20%. Fig. 1b plots response latency

Table 1							
Contrast-response	functions	for	grating,	plaid	and	barberpole	motions

(means \pm SD across motion directions and experiments) against grating contrast for the same subject. Similar relationships between contrast and latency were found for all three subjects. With the lowest grating contrast (2.5%), latency was of 108 ± 2 , 100 ± 4 and 110 ± 3 ms for subjects G.M., J.W. and S.J., respectively. It decreased rapidly as contrast increased, reaching the shortest values for mid and high contrast levels (e.g. 100% contrast: 85 ± 1 , 85 ± 2 and 88 ± 3 ms, same three subjects). The relationship between latency and grating contrast was best fit with an inverted Naka–Rushton function. The results will be described below, together with the latencies of responses to either barberpoles or plaids.

A sharp increase in response amplitude was observed when grating contrast increased from 2.5% to 20%, reaching saturation level with higher contrasts. This is evident from the family of velocity profiles, showing a rapid increase in initial eye velocity as contrast increases up to 20%. For grating contrast above 20%, initial eye velocity profiles overlapped altogether, indicating saturation in the initial eye acceleration. This non-linear relationship is illustrated in Fig. 1c where mean (across grating directions) changes in position over a (95-115 ms) time window are plotted against contrast, for subject GM. Continuous line plots the best-fit Naka-Rushton function. Similar data were observed for all three subjects and Table 1 summarizes best-fit parameters for each of them. Mean exponent and C_{50} values were of $1.6 \pm 0.2\%$ and $9.81 \pm 4\%$, respectively. These values were very consistent across subjects whereas the actual amplitude of the response (estimated by R_{max}) varied greatly. We performed a similar analysis using mean normalized data to evaluate the reliability of estimated parameters, irrespective of the absolute amplitude of ocular following responses. We found similar results: mean (\pm SD across conditions) C_{50} ranged between $17.4 \pm 4.8\%$ and $8.63 \pm 3.6\%$ (mean across subjects: $12.6 \pm 5\%$), which is not different from the C₅₀ estimated from the mean raw (i.e. not normalized) changes in ampli-

	Horizontal pos	sition (95–115 ms)		Vertical position (115–135 ms)				
	R _{max}	п	C ₅₀	<i>R</i> _{max}	п	C_{50}		
Single grating								
G.M.	0.058	1.35	14.14					
J.W.	0.045	1.58	6.14					
S.J.	0.013	1.72	8.96					
Unikinetic plaid	S							
G.M.	0.038	1.89	19.14	0.032	2.78	53.15		
J.W.	0.027	2.03	10.03	0.031	1.80	51.91		
S.J.	0.008	2.30	15.46	0.013	2.56	45.79		
Barberpoles								
G.M.	0.061	1.75	13.28	0.038	2.03	22.47		
J.W.	0.078	1.77	5	0.072	3.17	4.55		
S.J.	0.017	2.10	11.03	0.020	2.11	15.55		

Individual best-fit parameters for mean changes in horizontal or vertical position over the (95–115 ms) or (115–135 ms) time windows, respectively.

tude. Thus, idiosyncratic differences in response amplitude have no impact on the estimate of the main parameter of contrast gain control, its half-saturation contrast value.

Time-course of best-fit parameters illustrates the temporal dynamics of contrast gain control. Fig. 1d plots the best-fit curves obtained for each 20 ms temporal window, starting from 95 to 155 ms. We found a significant effect of the time windows on C_{50} values, for all grating directions (p = .0016). The inset plots the time-course of half-saturation contrast for all three subjects. Between the earliest and the latest time windows, mean C_{50} was halved (9.8 \pm 4% and 4.02 \pm 1.5%, respectively). A significant leftward shift (i.e. smaller C_{50}) of the contrastresponse function was observed between the first and second time windows (p = .008), but no further changes were evident with later time windows, except for a regular increase in the maximum response amplitude (i.e. R_{max}) due to eye acceleration. Thus, 135 ms after grating motion onset, there is no further enhancement of contrast gain.

3.2. 1D- and 2D-driven responses to unikinetic plaids

Fig. 2 illustrates the results obtained with unikinetic plaids when the total contrast of the pattern was varied from 2.5% to 100%. Fig. 2a plots, for one subject, the mean vertical and horizontal eye velocity profiles obtained when the plaid was the sum of a leftward drifting grating and a static oblique $(+45^\circ)$ grating. At high contrast, we observed the two response components previously reported by Masson and Castet (2002): an early component (latency \sim 85 ms) was initiated in the grating motion direction (i.e. 1D-driven component) and was followed by a late component (latency $\sim 105 \text{ ms}$) that rotated the ocular tracking toward the pattern motion direction (i.e. 2D-driven component). At very low contrast (<10%), this late component was absent and the 1D-driven component was delayed. Increasing plaid contrast induced both a reduction in vertical and horizontal latencies and an increase in both vertical and horizontal initial eye velocities. Fig. 2b plots the mean changes in horizontal (open symbols) and vertical (closed symbols) eye position, as a function of plaid total contrast. To take into account the ~ 20 ms latency difference found between early and late components, changes in horizontal and vertical eye positions were measured over two different time windows, (95–115 ms) and (115–135 ms), respectively. 1D-driven and 2D-driven components show different dependencies upon plaid contrast. The early component exhibits a steep contrast-response function, similar to that seen with single grating (Fig. 1c). C_{50} values ranged between 19.1% and 10% (see Table 1) and mean (across subjects) C_{50} and exponent were of $14.87 \pm 4.6\%$ and 2.1 ± 0.2 , respectively. When half-saturation contrast values for the 1D-driven responses were halved to illustrate the relationship between 1D-driven OFR and moving grating contrast (i.e. half of total plaid contrast), the mean values obtained (7.5 ± 2.3) were not significantly different from those found above in the single grating motion condition (p = .13).

On the contrary, there was a large difference between the contrast-response functions of 1D- and 2D-driven eve movements. Late, 2D-driven component showed a more linear dependency on plaid contrast with reduced exponents and very little saturation. Moreover, best-fit function was shifted to the right. Estimated half-saturation values ranged between 45% and 53% across subjects (mean C_{50} : $50.4 \pm 3.2\%$). Thus, there was a threefold increase in halfsaturation contrast values between the 1D- and 2D-driven response components (p = .0008). Again, to check that this difference was not due to some idiosyncratic changes in the eye acceleration, we performed the same analysis using normalized changes in amplitude of horizontal and vertical positions. We found similar mean (\pm SD across subjects and conditions) C_{50} values for both 1D- and 2D-driven responses $(15.9 \pm 6\%$ and $52.9 \pm 14\%$, respectively). No significant effect of motion direction was found (p = .416).

Fig. 3 illustrates the temporal dynamics of the contrastresponse functions of 1D- and 2D-driven eye movements. For all pairs of time windows, higher contrast gains were observed for the early, 1D-driven component (open symbols). These differences remained fairly constant over the whole open-loop period of tracking initiation, despite large variations in the response amplitudes. Thus, difference in contrast gain did not depend on which particular time window was chosen, as illustrated by the largely significant difference between C₅₀ values for 1D- and 2D-driven components with the latest time slice: $8 \pm 3\%$ and $37.7 \pm 10.6\%$, respectively (p < .001). Moreover, ones can see with subject S.J. that the difference in shape between contrast-response functions cannot be explained on the basis of the relative amplitude of 1D and 2D-driven responses. Finally, mean C_{50} values were halved for 1Ddriven component between the earliest (95-115 ms) and the latest (135-155 ms) time windows (14.9% and 7.9%), respectively, p < .05). For 2D-driven eye movements, mean C_{50} was reduced by ~25% but this difference was not significant.

3.3. 1D- and 2D-driven responses to barberpoles

Both early and late response components are elicited by barberpole motion where a drifting grating is presented behind a $+45^{\circ}$ tilted rectangular aperture. Earliest phase of ocular following is driven by 1D grating motion while later component is triggered by 2D line-endings motion with a 20-ms time delay (Masson et al., 2000). Fig. 4a illustrates the velocity profiles of horizontal and vertical responses to a barberpole motion, for the same subject as in Fig. 2. At very low contrast (2.5%), both components were delayed and vertical responses were almost negligible. Increasing contrast from 2.5% to 20% resulted in a shortening of response latency and an increase in initial eye velocity of horizontal responses. No further changes were observed for contrast above 30%. Nearly identical changes were observed for 2D-driven, vertical responses: a rapid increase followed by saturation for values above 30%. Response latencies decreased down to the values reported earlier for this late component (~105 ms). Relationships between latency and contrast will be further described below.

Amplitudes of each component have been measured over the two time windows illustrated by shaded gray bars in Fig. 4a, and are plotted in Fig. 4b. Contrast-response functions of early and late components were very similar, with a steep increase followed by an asymptote for contrast above 40%. Table 1 summarizes best-fit parameters for both responses components and for each subject. C_{50} values ranged between 13.3% and 5.01% for the 1D-driven response component and between 22.5% and 4.6% for the 2D-driven response components. There was no significant difference between half-saturation for 1D and 2D contrast-response function (p = .27). Across subjects, the mean C_{50} values were of $9.8 \pm 4.3\%$ and $14.19 \pm 9.5\%$, respectively. Moreover, half-saturation contrast for 1Ddriven component were not significantly different from those obtained with a single moving grating presented with a circular aperture as in the first experiment (p = .66). In brief, 1D- and 2D-driven responses to barberpole motion exhibit similar, steep contrast-response functions with saturation for middle contrast values. This result was clearly opposite to that found for the same time windows with unikinetic plaids. A similar analysis was again performed using the normalized data for each subject and condition. Mean (\pm SD) C_{50} values were of 12 ± 5.4 and 15.6 ± 9.5 , and were not significantly different.

Fig. 5 shows the temporal dynamics of contrastresponse functions for both 1D- (open symbols) and 2Ddriven (closed symbols) phase of ocular following. Despite large differences in response amplitude (see R_{max} , Table 1), all contrast-response functions exhibit similar shapes, irrespective of time windows. For later time bins, the responses were scaled up but the fundamental characteristics of the relationships between amplitude and contrast remained constant. There was a significant effect of the time window over which C_{50} was estimated for the 1D-driven components p = .031) but not for 2D-driven responses (p = .11). For 1D-driven responses, C_{50} were roughly halved between the first (95–115 ms) and the last (135–155 ms) time window (mean C_{50} : 9.8 ± 4.3 and 4.06 ± 3.2, respectively).

3.4. Comparison of contrast dynamics between plaid and barberpole motions

Fig. 6 plots the half-saturation contrast values (C_{50}) of the earliest contrast-response functions for both 1D- (open symbols) and 2D-driven (closed symbols) ocular following, for each subject and each type of motion stimulus. All 1Ddriven responses show a similar contrast dynamics, irrespective of the context in which the drifting grating is presented. When C_{50} was computed over the first time bin (95-115 ms) from the grating contrast alone (and not the total pattern contrast), we found mean (across subjects and directions) values of $7.5 \pm 2.3\%$, $11.9 \pm 5.4\%$ and $12.6 \pm 5.2\%$ for plaid, barberpole and grating motions, respectively (p = .11). For 2D-driven ocular following components, plaid and barberpole motions clearly resulted in different contrast-response functions. For all subjects, half-saturation contrast of responses to plaids were two or threefold higher than for gratings and barberpoles. Mean C_{50} (±SD across subjects and motion directions) for plaids and barberpoles were of $52.9 \pm 13.98\%$ and $15.61 \pm 9.61\%$ for the first (115–135 ms) time bin, corre-



Fig. 6. Temporal dynamics of contrast gain control for different 2D motions. Temporal evolution of the mean half-saturation contrasts (C_{50}) for 1D-(open symbols) and 2D-driven (closed symbols) response components to either plaids (a) or barberpoles (b) for each subject.

sponding to a threefold difference (p = .0002). We found no difference between motion directions (p = .77). This difference in contrast gain remained significant for the two other time windows (for instance, 155–175 ms, $C_{50} = 37.7 \pm 10.6\%$ and $6.8 \pm 3.2\%$, respectively, p = .0001).

To allow for a more direct comparison between the contrast-response functions of 1D- or 2D-driven ocular following obtained with either plaids or barberpoles, we normalized the changes in position and computed the mean across different 2D motion directions. In Fig. 7a-c, we plot these results, together with their best-fit functions, on the same graph for each subject. Open and closed symbols illustrate the 1D- and 2D-driven ocular following component, respectively, for barberpole (green) and plaid (red) and with the earliest time bins. All 1D-driven components were identically affected by moving grating contrast. On the contrary, contrast-response relationships for 2D-driven components were very different: a sluggish contrastresponse curve linked stimulus contrast and ocular responses to plaids whereas a very brisk contrast-response function was found for barberpoles. The difference between half-saturation contrast values are further illustrated in Fig. 7d, where mean C_{50} values are plotted together to show the 3-5 times difference observed between barberpole and plaid motions.

3.5. Comparison of temporal dynamics for plaid and barberpole motions

We measured relationships between horizontal and vertical latencies and stimulus contrast. We first report the results obtained with plaid motion. Fig. 8a plots the mean latencies (\pm SD, across plaid motion directions) of both horizontal (open symbols) and vertical (closed symbols) responses against total plaid contrast, for each subject. At the lowest plaid contrast, latency of vertical eve movements cannot be measured. At 5% contrast, mean latency difference between horizontal and vertical responses ranged from 29 ± 6 to 22 ± 3 ms across subjects. At the other end of the contrast range (between 80% and 100%) this mean difference ranged from 21.5 ± 2 and 12 ± 7 ms. Latencies of 1D- and 2D-driven responses decayed towards different asymptotic values, illustrating the 15-20 ms delay found between initiations of early and late phases of ocular following (Masson & Castet, 2002). Mean (±SD across subjects and directions) latency for horizontal and vertical responses were of 87 ± 4 and 103 ± 5 ms, respectively (p = .0001). This difference was not affected by motion direction (p = .46). Similar results were observed with barberpole motion (Fig. 8b). Early and late component latencies exhibited a similar decay with increasing contrast. At



Fig. 7. Contrast-response functions for normalized changes in position. (a–c) Mean (\pm SD across directions) normalized changes in horizontal (open symbols) and vertical (closed symbols) eye positions are plotted against total stimulus contrast for barberpoles (green) and plaids (red), for the three subjects. Continuous lines are best-fit estimate of Naka–Rushton functions. (d) Mean (\pm SD across directions) best-fit C_{50} are plotted for the two conditions, and each subject. Black bars, plaids; grey bars, barberpoles.



Fig. 8. Contrast dynamics of ocular following latencies. For each subject, mean (\pm SD across directions) latencies of 1D- (horizontal) and 2D- (vertical) driven responses are plotted against contrast, for plaid (a) and barberpole motions (b). Continuous lines are best-fit inverted Naka–Rushton functions.

very low contrast (5%), mean (across directions) latency difference between horizontal and vertical responses ranged from 36 ± 13 (G.M.) and 25 ± 6 ms (J.W.). At high con-

trast (between 80% and 100%), the difference ranged between 20 ± 1 (G.M.) and 14 ± 4 ms (S.J.). Thus, relationships between response latency and contrast converged

towards a significant difference between asymptotic values of ~20 ms (mean across subjects and directions, 86 ± 2 and 102 ± 2 ms, for early and late, respectively, p = .0001), confirming the previous study by Masson et al. (2000). No significant effect of motion direction was found on latency difference (p = .98). Moreover, no significant difference was found between latencies of late components elicited by either plaid or barberpole motion (p = .435).

To illustrate that both types of 2D motion stimuli produced similar temporal dynamics, we plotted 2D latencies against 1D latencies, for all contrast values (Fig. 9) and for plaid (closed symbols) and barberpole (open symbols) motions. Diagonal dashed lines illustrate the unity relationship. One parallel line is also plotted for each graph, with a vertical offset computed from the individual mean latency difference across contrast and motion types, as indicated by numbers. For the three subjects, these mean (\pm SD across directions and contrasts) latency differences were of 26 \pm 5 (G.M.), 21 \pm 6 (J.W.) and 18 \pm 8 ms (S.J.) with plaids and of 24 \pm 9 (G.M.), 19 \pm 5 (J.W.) and 19 \pm 7 ms (S.J.) wit barberpoles. The fact that all pairs were scattered along these lines indicates that early and late response have similar dependencies on contrast but are delayed by a fixed amount. Nevertheless, the latency difference was somewhat larger (but also more variable) with low-contrast motions (right-end of the curves).

To fully describe the contrast dynamics, we fitted inverted Naka–Rushton functions (continuous lines in Fig. 8) to the latency-contrast data and estimated several parameters (see Table 2): the overall changes in latency (τ_{shift}) , the exponent of the latency decay (*n*) and the latency shift half-saturation (S_{50}). Again, we obtained similar parameters for either single grating, plaid or barberpole motion when considering the earliest component of ocular following. Average (\pm SD) S_{50} were of $8 \pm 1.5\%$, $6.4 \pm 0.8\%$ and $7.5 \pm 0.3\%$, respectively. Average τ_{shift} were of 20.2 ± 4.8 , 34.2 ± 7.6 and 22 ± 4.6 ms, for the same conditions, indicating a similar decay of latency with increasing contrast, irrespective of type of motion stimulus. Lastly, exponents of the inverted Naka–Rushton functions were also very similar (see Table 2).



Fig. 9. Timing difference between 1D- and 2D-driven ocular following. For each subject, horizontal and vertical latency are plotted one against another, for each stimulus contrast. Open and closed symbols are results for barberpole and plaid motions, respectively. Oblique dotted lines indicate the unity relationship without or with a constant latency difference shift, as indicated by numbers.

Table 2

	Horizontal	latency		Vertical latency				
	$ au_{\max}$	$ au_{ m shift}$	3	S_{50}	$\tau_{\rm max}$	$ au_{\mathrm{shift}}$	3	S_{50}
Single grating								
G.M.	110	24	1.66	7.7				
J.W.	101	16	1.57	9.6				
S.J.	111	22	1.96	6.7				
Unikinetic plaid	ls							
G.M.	122	36	1.80	6.92	141	42	1.20	27.21
J.W.	110	26	2.37	6.73	125	23	3.03	19.50
S.J.	132	41	2.41	5.50	144	49	1.19	21.56
Barberpoles								
G.M.	111	27	2.04	7.9	165	36	1.80	6.92
J.W.	102	18	1.70	7.4	136	35	1.44	7.88
S.J.	109	21	1.93	7.3	157	21	1.53	7.26

Best-fit parameters for mean changes in horizontal or vertical latencies of ocular following responses to grating, plaid and barberpole motion stimuli

As illustrated by continuous lines and closed symbols in Fig. 8a and b, relationships between latencies of 2D-driven responses and contrast were different between plaids and barberpoles. With barberpole stimuli, the latency were reduced by $\sim 31 \text{ ms}$ over the 2.5–100% contrast range (mean τ_{shift} : 30.7 \pm 8 ms) and mean half-reduction contrast (S_{50}) was of $7.3 \pm 0.5\%$ which is not significantly different from the values observed for the 1D-driven component. With plaids, however, mean (\pm SD across subjects) estimate of S_{50} were threefold higher for 2D- than for 1D-driven responses $(22.8 \pm 4\%)$ and $6.4 \pm 0.8\%$ respectively, p = .005). The comparison between best-fit parameters obtained for either response latency (S_{50} and exponent) or amplitude (C_{50} and exponent) shows that the two functions have similar slopes and half-saturation contrast. This result indicates that both latency and amplitude followed the same dependency upon contrast, albeit with a different gain factor. This is also supported by the comparison between half-saturation contrast values obtained with either 1D- or 2D-driven responses with plaids: contrastresponse functions for latency and amplitude exhibited a threefold increases in either S_{50} or C_{50} , respectively.

3.6. Factoring out latency from amplitude effects

Estimating response amplitudes from changes in eye position may confound changes in latency with changes in initial eye velocity due to contrast level. Eye velocity profiles displayed in Figs. 2a and 4a show that increasing contrast both lowered response latency and increased initial eye velocity as indicated by the different slopes of eye velocity profiles. We computed eye acceleration from mean eye velocity profiles, for each stimulus condition. Fig. 10 illustrates these acceleration profiles, for two subjects with either unikinetic plaids (Fig. 10a) or barberpoles (Fig. 10b). Left-side plots are horizontal eye acceleration. Increasing contrast from 2.5% to 10% resulted in a sharp increase of initial horizontal acceleration. Higher contrast (range displayed 10–40%) did not further boost the initial eye acceleration. Right-hand plots show eye acceleration

profiles along the vertical direction, i.e. the acceleration of 2D-driven components. With unikinetic plaids, increasing contrast from 2.5% to 40% resulted in regularly spaced profiles, indicating slowly increasing initial eye acceleration. On the contrary, a similar contrast increase resulted in a sharp increase in eye acceleration (contrast range: 2.5-10%) followed by saturating ocular responses for contrast higher than 20%. Thus, increasing total contrast of either a plaid or a barberpole resulted in different changes in initial eye acceleration.

We quantified this difference by plotting the mean peak of acceleration against contrast for both horizontal and vertical components (Fig. 11) and fitting the results with Naka-Rushton functions for each subject (Table 3). We found that, for plaids, C_{50} values were much larger for vertical (i.e. 2D-driven) than for horizontal (i.e. 1D-driven) eve acceleration (means \pm SD: 25.3 \pm 13 and 4.8 \pm 0.7, respectively). No significant differences were found between best-fit exponents. On the contrary, with barberpoles, C_{50} values were only marginally larger for vertical (i.e. 2D-driven) than for horizontal (i.e. 1D-driven) response components (means \pm SD: 4.8 \pm 1.3 and 3.1 \pm 0.4, respectively). Again, exponents were not significantly different between conditions. Overall, best-fit parameters obtained for horizontal eye accelerations were not significantly different between single grating, unikinetic plaid and barberpole motions. Thus, results obtained with initial peak acceleration were very similar to those reported above with response amplitude over fixed time windows. Lastly, we analyzed the time of occurrence of the acceleration peak, across the whole range of contrast. Time-to-peaks, for each condition and observer, are plotted against contrast in Fig. 11a and b and were well fitted with the inverted Naka-Rushton function. We found a mean difference between times of occurrence for horizontal and vertical acceleration peaks of 22 ± 6 (plaid patterns) and 21 ± 6 ms (barberpoles), confirming the latency analysis reported above. Such difference remained largely constant across the contrast range investigated as shown by the largely parallel best-fit functions.





Fig. 10. Acceleration profiles for horizontal and vertical eye movements. For two subjects (G.M., J.W.), eye acceleration profiles are plotted for six total contrast values for both horizontal and vertical directions. Calibration bars indicate an acceleration of 50°/s/s for all plots. Ocular following responses to either plaids (a) or barberpoles (b) with both pattern motions along the rightward-upward directions.

3.7. A two-pathway Bayesian model of motion integration

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To summarize, we have shown that 1D- and 2D-driven ocular following responses can have very different contrast

dependencies but exhibit a remarkable latency pattern: both 1D- and 2D-response latencies decay with increasing contrast but 2D-driven responses are delayed by \sim 20 ms relative to 1D-driven responses, irrespective of the shape



Fig. 11. Relationships between either acceleration peak or time-to-peak and total contrast. (a) Ocular following responses to plaids (a) or barberpoles (b). Continuous lines are best-fit Naka–Rushton function (acceleration peak) or exponential decay function (time-to-peak). For relationships between time-to-peak and contrast, data from each subject are overlapped to illustrate variability across subjects.

Table 3			
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Individual	best-fit	t parameters	for mean	acceleration	peak in	horizontal	or vertical	directions,	respectively,	for each	type of	motion	stimulus

	Horizontal acc	eleration peak		Vertical acceleration peak				
	R _{max}	п	C_{50}	R _{max}	п	C ₅₀		
Single grating								
G.M.	160	2.32	2.58					
J.W.	103	3.23	2.41					
S.J.	34	1.72	2.86					
Unikinetic plaids								
G.M.	141	2.14	5.64	109	2.03	12.44		
J.W.	101	1.97	4.81	93	1.33	39.27		
S.J.	41	1.61	4.13	33	1.27	24.05		
Barberpoles								
G.M.	160	1.23	3.52	105	1.83	6.21		
J.W.	132	1.84	2.90	132	2.54	3.52		
S.J.	64	1.56	2.72	53	1.67	4.70		

of their contrast-response functions. In particular, 1D- and 2D-driven responses to barberpole motion have identical contrast-response relationships for either amplitude or latencies but still a constant difference of ~ 20 ms was found between their latencies. A two-pathway model of motion integration (e.g. Löffler & Orbach, 1999; Wilson, Ferrera, & Yo, 1992) could easily explain the latency difference by having a fixed additional delay within the 2D pathway. The parallel latency-contrast relationships found for

both 1D and 2D responses argue for a single mechanism that sets response latency independently of response amplitude (Miles et al., 1986). Moreover, the fact that 1D and 2D contrast-response functions were very similar for barberpole motions support a single contrast gain control for 1D- and 2D-driven responses. However, we still need to explain the flatter contrast-response function of 2Dresponses to plaids when compared to barberpoles, although total contrast of 2D features (blobs and line-endings) was similar. Assuming a single 2D extraction mechanism we propose that a flatter contrast–response function reflect a less reliable 2D velocity estimates in the former case (see Hürlimann, Kiper, & Carandini, 2002, for a similar approach with the perceived speed of grating motion). To test such hypothesis, we designed a modified version of the Bayesian model of motion integration proposed by Weiss et al. (2002).

3.7.1. Modeling the oculomotor response

The oculomotor response was modeled as the response of an ideal observer using a probabilistic representation of motion information, which is computed using Bayes' Theorem. Such a model of motion integration assumes that the different motion cues present in the flow of images are independently represented by different probability distributions in the velocity space (velocity likelihoods). The uncertainty about the velocity of a given cue is reflected by the variances of the distribution along the different directions (Simoncelli, Adelson, & Heeger, 1991; Simoncelli & Heeger, 1998). The stimulus velocity is then inferred by multiplying these velocity likelihoods with an *a priori* knowledge known as a prior distribution in the same velocity space. This product is a posteriori distribution. Weiss et al. (2002) proposed that such prior distribution takes the form of a Gaussian distribution centered onto the null velocities. The best estimate of target velocity is then given by the maximum of the *a posteriori* probability distribution (MAP). Their model renders many of the misperceptions (i.e. biases in direction or speed perception) observed with plaid or line motions and how they vary with contrast. Similarly, applying such a Bayesian model to ocular following assumes that initial amplitude of oculomotor responses is proportional to the target velocity as read out from the a posteriori distribution. Response dynamics (i.e. relationships between amplitude and latency and contrast) can then be explained by the dynamics of this distributed representation when using a linear population decoding mechanism such as a vector average (Priebe & Lisberger, 2004; Takemura, Inoue, Kawano, Quaia, & Miles, 2001).

3.7.2. Extracting 1D and 2D motion cues

A major change with the model of Weiss et al. (2002) is the assumption that 1D and 2D features are extracted independently through two simple mechanisms with different delays. This architecture is consistent with our findings that there is a nearly constant 20 ms timing difference between 1D- and 2D-driven response components and that both latencies follow similar dependency upon contrast. Extracting 2D motion through some non-linear operators is also needed to reconstruct barberpole and unikinetic pattern motion as only one single 1D motion was present in all stimuli and therefore that the IOC rule cannot be applied (Löffler & Orbach, 1999). As in Weiss et al. (2002), the motion extraction stage was based on a generative model of the full-field translation of the visual scene, which may be related to classical image processing technique (see Fleet & Weiss, 2005, Chapter 15). One-dimensional motion input was computed after low-pass filtering in space and a twopoint differentiation in time. Two-dimensional motion cues were extracted by selecting local maxima through a nonlinear operation (see Appendix A). Such operation is similar to the filter-rectify-filter scheme proposed for extracting texture cues and computing their motion (Wilson et al., 1992). More important, characteristics of 1D and 2D motion extraction stage were kept fixed when processing all images so that likelihoods were computed in exactly the same way for all motion stimuli. Another key point here is that no specific contrast gain control mechanism was implemented. Likelihoods for 1D and 2D cues are illustrated in Fig. 12b in a polar plot with log-scale for the probability value.

3.7.3. Contrast–response functions and parallel, distributed representations

Increasing the contrast was modeled by proportionally decreasing the noise's standard deviation. High contrast values thus resulted in a sharper *a posteriori* probability distribution (Fig. 12c) for both 1D and 2D pathway. Clearly, the *a posteriori* 2D distributions were centered onto the actual 2D velocity of the moving patterns. Such a direction cannot be extracted from 1D distributions since patterns were made with only one edge motion. At low contrast, very different distributions were observed between plaid and barberpole motions. Line-endings motion still produced a narrow distribution centered near the actual velocity ($v_x = v_y = 1$) of the motion input. On the contrary, for the same total contrast (10%), an unikinetic plaid resulted in a very broad distribution whose mean value was centered onto a much slower velocity. We fitted our model to the average normalized data to estimate the values of the two model parameters that would best render the various relationships between ocular response amplitude and contrast.

Results are illustrated in Fig. 13a and c where mean normalized amplitude of the horizontal and vertical responses are plotted against contrast, for each type of motion stimulus. Continuous lines are best-fit contrast-response functions computed with our model. Fig. 13a illustrates both data and model for the 1D-driven component. The best χ^2 values were obtained for σ values between 5.8 and 7.4 for grating motion and of 18.3 and 5.3 for 2D motion with either plaids or barberpoles, respectively. Best-fit C_{50} were of 9% (grating), 13.9% (plaids) and 9.3% (barberpole), which are not significantly different from the estimates obtained with the Naka-Rushton function (see Table 1). In the same vein, for 2D-driven responses, best-fit C_{50} values were of 53.2% and 11.6%, for plaids and barberpoles, respectively. Again, these estimates were very similar to both those given in Table 1. Of particular interest, it must be noticed that using identical a priori hypothesis (i.e. identical 1D and 2D filtering and Prior distributions), we obtained a similar ratio between C_{50} of either pathways



Fig. 12. A two-pathway Bayesian model. The three computational steps to extract parallel, distributed representations of 1D and 2D motion cues are illustrated for a plaid (left-hand panels) and a barberpole (right-hand panels). (a) Outputs of the initial filtering stage extracting 1D and 2D motion features. (b) Likelihood distributions in the velocity space (v_x, v_y) are plotted for each pathway, together with a common prior distribution centered at (0,0). (c) *A posteriori* probability distributions of 1D and 2D motion signals at both low (10%, top row) and high (40%, bottom row) contrast.

for both unikinetic plaids (best-fit ratio: 3.8; mean observed ratio: 3.6) and barberpoles (best-fit ratio: 1.2; mean observed ratio: 1.3).

Although our algorithm is very simple and performed quite well to fit experimental data (Fig. 13), it is analytically intractable. As in Weiss et al. (2002), we may assume that the log-likelihood is quadratic. Assuming Gaussian distribution for likelihoods, we can analytically demonstrate that a Naka–Rushton function with exponent of 2 will necessarily fit our contrast–response functions. In fact, the *a posteriori* log-probability distribution function may then be written as:

$$\log P(\vec{v}|i) = -\log Z - \frac{1}{2} \left[C^2 \cdot \frac{\|\vec{v} - \vec{v}_o\|}{\sigma^2} + \frac{\|\vec{v}\|^2}{\sigma_p^2} \right]$$
(1)

where Z is a normalization constant which does not depend on target velocity, \vec{v}_0 and σ are, respectively, the mean and standard deviation of the likelihood distributions and σ_p is the Prior's standard deviation. One should note that the *Maximum A Posteriori* (MAP) is strictly equal to the mean for Gaussian distribution. This is therefore equivalent to compute the vector average of the different motion signals present in the image. The solution of the Ideal observer satisfies:

$$\frac{\mathrm{d}}{\mathrm{d}\vec{v}}\log P(\vec{v}|I) = \frac{C^2}{\sigma^2}(\vec{v}_{\mathrm{m}} - \vec{v}_{\mathrm{o}}) + \frac{\vec{v}}{\sigma_{\mathrm{p}}} = 0$$
⁽²⁾

that is

$$\vec{v}_{\rm m} = \frac{C^2}{C^2 + C_{50}^2} \vec{v}_{\rm o} \quad \text{with } C_{50}^2 = \frac{\sigma^2}{\sigma_{\rm p}^2}.$$
 (3)

Hürlimann et al. (2002) suggested a similar formulation. The quadratic approximation involves necessarily that all contrast–response functions follow a Naka–Rushton function with exponent of 2. It should be noted that these functions are ideal to model contrast–ocular response relationships because they are monotonous functions (increase contrast should give an increase in response), give no response for 0 contrast (a zero contrast stimulus should give a null ocular response) and saturate to the actual maximal response amplitude (Masson & Castet, 2002; Sheliga et al., 2005). With an exponent of 2, they have only one free parameter: the contrast at half saturation C_{50} . In a Bayesian framework, the value of this parameter corresponds to the point where *a priori* and likelihood information are bal-





Fig. 13. Model fitting of contrast-response functions. The mean normalized change in horizontal (a) and vertical (c) position are plotted as a function of contrast of 1D and 2D motion signals, respectively. Continuous lines plot the best-fit model output. Broken lines plot the best-fits obtained when constraining a Naka-Rushton function with an exponent of 2. Each motion stimuli are presented with different colors. The best-fit estimates of halfsaturation contrast (C_{50}) are plotted against the parameter K to illustrate the time course of contrast dynamics for both 1D- (b) and 2D-driven (d) ocular response components.

anced. Moreover, the tangent of this function at the C_{50} value (where the ocular response approaches the linear regime) crosses the abscissa at the origin (or at a contrast value of $(1 - \frac{2}{n})C_{50}$ for an exponent of *n*). The same dataset was fitted with a constrained Naka-Ruston model (with n = 2). Best-fits are illustrated in Fig. 13a and b as broken lines. No significant difference was found between the complete and reduced model even for the 2D cues with the barber pole stimulus, which is characterized by a bimodal velocity likelihood. This suggests that more important than the actual shape of the velocity likelihood, it is its first two moments that are crucial for motion integration.

3.7.4. Temporal dynamics

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A single non-linear threshold mechanism cannot explain the 20-ms time difference between 1D and 2D components since it is independent upon contrast and similar for barberpoles and plaids despite the different contrast-response functions. However, we found that the relationship between latency and contrast can be best fitted with an inverted Naka-Rushton function. This model, relating the noise in the 1D and 2D likelihoods and the latency is similar to the trigger mechanism originally proposed by Miles et al. (1986) for ocular following in monkeys. Lastly, when integrating in a longer time window Δt and assuming that noise is independent over time, we found that under the quadratic approximation, C_{50} is inversely proportional to Δt (see also Weiss et al., 2002). With $\sigma_{\rm p}$ being fixed, we can estimate the effects of temporal integration on both 1D- and 2D-contrast-response functions as found for eye movements (Figs. 1 and 6). Fig. 13b and d plots the bestfit C_{50} values obtained with our model when varying the width of the integration window (K) following the formula: $C_{50}^2 = C_{50i}^2 / K$ where C_{50i} is the initial half-saturation values obtained for a small, arbitrary integration window (Δt) and K is an increasing number of (Δt) . We obtained a hyperbolic decay of C_{50} , similar to the effects of temporal integration upon contrast dynamics as observed with both single gratings (Fig. 1), plaids and barberpoles (Fig. 6). Thus, our model accounts for the temporal dynamics of contrast-response functions by varying only one parameter that reflects the time scale of motion integration.

4. Discussion

The present study further demonstrates that the initiation of short-latency ocular following reflects the dynamics of motion integration. First, we show that early and late tracking components have similar temporal dynamics with different 2D motion stimuli such as plaids and barberpoles. This suggests that the temporal dynamics of late ocular tracking, and therefore of, presumably, the neural solution for 2D motion integration is independent on the type of 2D cues present in the motion stimulus. Second, we demonstrate that this delayed dynamics cannot be explained on the sole basis of different contrast sensitivities: different contrast-response functions yield to nearly identical temporal dynamics. Third, we show that a two-pathway Bayesian model of motion integration render most of these results with a very small set of parameters. In particular, having different contrast-response functions reflect the dynamics of independent distributed motion representations fed by 1D and 2D motion inputs and their evolution with time. A single 2D features motion processing was used for all motion stimuli. Assuming a fixed timing difference between 1D and 2D-driven responses, the model could also take into account the temporal dynamics of motion integration.

4.1. Temporal dynamics of 2D ocular tracking

When presented with either unikinetic plaids or barberpoles at full contrast, ocular responses can always be decomposed into an early component which is driven by grating motion at latency \sim 85 ms and a late component which is elicited $\sim 20 \text{ ms}$ later and deviates tracking towards the 2D global motion direction. We call them 1D- and 2D-driven ocular following components. This temporal dynamics is independent on how global motion is computed since latencies of the 2D-driven component in both conditions are strictly similar over a large contrast range. Moreover, the latencies of 1D- and 2D-driven components vary similarly with contrast. The latency of the earliest, 1D-driven component rapidly decreases in a nonlinear way from ~ 110 to ~ 85 ms when grating contrast increases only from 2.5% to \sim 40–50%. To our knowledge, this is the first description of such a very steep latency-contrast relationship for ocular following in humans. Miles et al. (1986) reported similar results in macaques, albeit on a different range of latencies (80-55 ms) as ocular following responses are faster in monkeys. The 2D-driven component is delayed by ~ 20 ms at high contrast, for both barberpoles and plaids. Lowering the contrast increases the latency of this 2D-driven component, for both types of motion. In fact, the latencies of responses to either barberpoles or plaids are very similar over a large range of contrasts, further demonstrating the similar temporal dynamics of ocular following responses to both types of motion stimuli. Except at the lowest contrast values

(<10%), where late components are nearly absent, this delayed latency is inversely related to stimuli contrast.

It shall be noticed that previous work on ocular following responses to either barberpole or unikinetic plaid motion have shown that similar temporal dynamics was observed when rotating grating motion by 90° (Masson & Castet, 2002; Masson et al., 2000). In the latter condition, 1D motion direction is now along the vertical axis while contribution of 2D motion signals can be seen, after a 20 ms time delay, in the horizontal eve velocity profiles. Moreover, the differences found in the modulation of 1Dand 2D-driven responses when varying the relative contrast between drifting and static components of an unikinetic plaid were similar for both vertical and horizontal grating motion directions (Masson & Castet, 2002). These results strongly suggest that both the temporal dynamics and the contrast dynamics of early and late components of ocular following cannot be attributed to some anisotropies in the oculomotor plant. Instead, we propose that the behavioral differences reported herein reflect the different contrast dynamics of 1D and 2D biological visual motion computations.

4.2. Contrast dynamics of 1D-driven tracking

The amplitude of these two tracking components varies with contrast in a very robust, non-linear way. The 1D-driven component always exhibit a very steep contrastresponse function where half-saturation is reached at contrast $\sim 10\%$ and that saturates for contrast above 30–40%. In a recent study, Sheliga et al. (2005) found very similar contrast-response functions in human using square-wave gratings. This very steep, non-linear relationship mimics many of the properties of the Magnocellular pathway: LGN M-cells exhibit a steep dynamics with median C_{50} $\sim 10\%$ and exponent ~ 1.2 (Sclar et al., 1990). Lower C_{50} (range: 5–20%) and steeper exponents (\sim 3) were found for area MT neurons (Heuer & Britten, 2002; Kohn & Movshon, 2003; Movshon & Newsome, 1996; Sclar et al., 1990). Thus, there is a strong consistency between these physiological properties and our behavioral results, suggesting that the main driving input of the earliest phase of ocular following originates from the Magnocellular input to area MT. This idea is consistent with both the critical role of the MT/MST complex for ocular following initiation (Kawano, 1999; Takemura, Inoue, & Kawano, 2002) and the fact that Magnocellular-driven V1 neurons are the main direct input to area MT (Movshon & Newsome, 1996; Yabuta, Sawatari, & Callaway, 2001). It is also consistent with the fact that earliest phase of ocular following is driven by linear, luminance-based 1D motion detection (Masson & Castet, 2002; Masson et al., 2002; Sheliga et al., 2005). Finally, we found very little change of the 1D contrast-response function when measured at different epochs during the open-loop phase of tracking initiation. This indicates that grating-driven ocular following exhibits very little temporal integration and relies on a neural processing which sets very early and quickly its response dynamic range. This observation is consistent with a recent study by Albrecht et al. (2002) who showed that V1 neurons of macaques exhibit a very brisk temporal dynamics where a single—but scaled—Naka–Rushton function could be used to fit the response characteristics measured either very early or very late from the neuronal discharge pattern. No similar data are yet available for monkeys MT neurons.

4.3. Contrast dynamics of 2D-driven ocular following

The initial phase of the 2D-driven responses to unikinetic plaids show a more sluggish, quasi-linear contrastresponse function with mean $C_{50} \sim 53\%$, mean exponent \sim 1.8 and an absence of clear saturation. At very low contrast, pattern-motion is almost invisible to the tracking system and responses are dominated by grating motion. Above 10% contrast, a significant late component begins to be seen and increases linearly with plaid contrast. These properties are very similar to those reported for LGN Parvocellular neurons, with median $C_{50} \sim 50\%$ and exponent \sim 1.6 (Sclar et al., 1990) and this led us to suggest earlier that late component might be primarily dependant upon Parvocellular-like inputs to the 2D motion computation stage (Masson & Castet, 2002). However, if 2D motion directions were computed from a single mechanism, similar contrast-response functions for the late phase of tracking responses to either plaids or barberpoles should be observed. Clearly, we found the opposite result. With barberpoles, mean C_{50} and exponent are of ~16% and ~4, respectively and responses saturate for contrast above 30–40%. The shape of these functions is very similar to that observed for grating-driven responses. Therefore, our results show that different contrast-response functions of 2D-driven tracking component can lead to very similar temporal dynamics. This, together with the fixed lag observed between 1D- and 2D-driven components over a very large contrast range, argues against the idea that the delayed latency of 2D-driven component can be explained by a poorer contrast sensitivity of the underlying mechanism.

4.4. A distributed representation of 1D and 2D motion integration

Different computational rules have been proposed for 2D motion integration. For some 2D moving patterns, such as Type I plaids, the vector average (VA) of the different 1D motions can indicate the actual pattern motion direction (Ferrera & Wilson, 1990). Within a two stages motion computation, a detection stage extracts motion orthogonal to each 1D edge and feeds an integration stage, which computes the VA solution. Contrast gain control is set at the earliest stage and therefore component- and pattern-driven responses exhibit the same dependency upon contrast. When the VA solution fails to reconstruct the true

pattern motion, the Intersection of Constraint (IOC) (Adelson & Movshon, 1982; Movshon, Adelson, Gizzi, & Newsome, 1985) and the 2D feature tracking (2DFT) rules (e.g. Alais, Wenderoth, & Burke, 1997; Gorea & Lorenceau, 1991; Mingolla, Todd, & Norman, 1992) can always be used to recover the true 2D pattern motion. The IOC rule postulates similar (but scaled) contrast-response functions for plaid and grating motion perception (Stone, Watson, & Mulligan, 1990). This is clearly not the case herein. Wilson et al. (1992) have suggested an intermediate model where periodical first- and second-order motions are extracted separately and then combined. Löffler and Orbach (1999) subsequently demonstrated that this twopathway model computes the global direction of tilted lines and barberpoles. However, although this model could explain the temporal dynamics of motion integration, it cannot explain why different contrast-response functions are observed herein with either plaids or barberpoles as a single contrast gain control is arbitrarily set early for all motion computation (Löffler & Orbach, 1999; Wilson et al., 1992). Finally, the 2DFT scheme proposes that localized, 2D elements are extracted before that their unambiguous motion is computed and integrated with ambiguous 1D motion signals in order to recover surface motion (e.g. Gorea & Lorenceau, 1991; Lorenceau et al., 1993; Mingolla et al., 1992; Power & Moulden, 1992). In principle, the 2DFT rule postulates that 1D and 2D motion computations have different gain control elements but no direct physiological evidence is yet available to support this assumption. In fact, we show herein that different contrast responses are found with different 2D features, arguing against a single gain control mechanism.

In brief, there is no unified computational framework that could account for our behavioral results and resolves the following apparent contradiction: the 2D-driven tracking component to different motion stimuli can exhibit both similar temporal dynamics and different contrast-response functions. Our computational study shows that within a single framework one can builds independent, distributed representations of 1D and 2D motion and scales the ocular response differently for each type of motion stimulus. Our model can be seen as a probabilistic version of the two-pathway motion model. However, it does not assume any early contrast gain control mechanism (see Wilson et al., 1992). Moreover, it uses a unique filtering and motion computation scheme for the 2Dmotion pathway, based on features extraction (see Del Viva & Morrone, 1998; Wilson et al., 1992) and uses one single set of parameters for all types of motion stimuli. This is sufficient to render the dynamics of motion integration: the different contrast-response functions reflect the different dispersion of motion signals within a single distributed representation. To scale the response amplitude with contrast, we implemented a Bayesian model with a prior centered at the origin of the velocity space (Weiss et al., 2002). Within this probabilistic framework, parameters of the contrast-response function can

be seen as a ratio of the variance of the Prior and Likelihood distributions (see also Hürlimann et al., 2002). Such a simple Bayesian model renders the main characteristics of our results and opens the door for a time-dependent model incorporating different latencies for each distributed representation. It provides a first direct evidence for linking different computational approaches of contrast gain control through the same set of behavioral data and will enable further quantitative investigation of motion integration using tracking eye movements.

Our approach differed from the model of Weiss et al. (2002) in several ways. First, the two-pathway architecture provides an explicit implementation of the different visual motion mechanisms that extract either 1D or 2D motion cues. We used a general framework for filtering images and extracting 1D and 2D cues, using a luminance conservation constraint (Perrinet, Barthélemy, Castet, & Masson, 2005). On the contrary, the model by Weiss et al. (2002) implement the IOC rule and therefore postulates only one pathway. This single motion pathway cannot account for the timing difference between 1D- and 2D-driven responses. Second, our model does not make any assumption regarding both the shape of the constraint function and the resulting contrast-response function is in general analytically intractable. Thus, depending on the sharpness of the likelihood probability distribution, we can obtain a rich family of different curves. In particular, an higher kurtosis enables to render contrast-response functions that would be otherwise fitted with Naka-Rushton functions with exponents higher than 2. On the contrary, under the assumption that log-likelihood probability follows a Gaussian distribution (Weiss et al., 2002), contrastresponse functions would be only modeled by Naka-Rushton functions with an exponent of 2 (see also Hürlimann et al., 2002). Such assumption is obviously inappropriate for a large family of results, in particular the ocular following responses to barberpoles. Thus, our model was very efficient to render individual and average behavioral data and consequently forms a promising framework for modeling ocular following responses to more complex stimuli such as center-surround interactions (Barthélemy et al., 2006).

5. Conclusions

Using ocular following responses in humans, we have shown that the delay between 1D- and 2D-driven responses cannot be explained from different contrast gain controls such as found between high and low spatial frequency channels. On the contrary, similar temporal dynamics of late ocular tracking can be found with different contrast– response functions. This suggests that there is indeed an additional delay for extracting 2D motion cues and therefore computing the 2D global motion of a visual surface. Moreover, using a Bayesian model of motion integration, we show that initial eye acceleration reflects the dynamics of the distributed representations of local 1D and 2D signals in the motion pathway. Thus a single motion mechanism can be responsible for extracting 2D signals and driving the eye movement responses towards surface motion direction.

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Appendix A

We describe herein the image processing steps that were applied for each pathway (also called 1D and 2D pathways) before computing the velocity likelihoods for 1D and 2D motion cues. We also give the algorithms applied to our stimuli, as Matlab source code.

A.1. Image whitening

We first applied a linear filtering to ensure that every spatio-temporal frequency was given the same weight. This step is crucial for handling natural images where different frequencies coexist and is used in general in our models of the primary steps in the visual processing stream (e.g. Olshausen & Field, 1998; Perrinet, 2007). It corresponds to convoluting the signal with a spatio-temporal kernel whose Fourier spectrum linearly increases with the frequency up to a cut-off frequency to avoid noise amplification. It is also called a de-correlation filter because natural images have a mean Fourier spectrum inversely proportional to the frequency, and the output of this process is therefore whitened in average. Temporal de-correlation was approached by a simple ARMA process.

The Matlab code for our implementation of this step is given below:

% Spatial de-correlation
for i_frame=1:n_frame,
$I_m_K(:,:,i_frame) = conv2(I_m(:,:,i_frame),K,'same');$
end;
% temporal decorrelation
$I_m_K(:,:,3:n_frame) =1*I_m_K(:,:,3:n_frame)$ -
.5*I_m_K(:,:,2:n_frame-1)+ I_m_K(:,:,1:(n_frame-2)),

A.2. Image motion computation

More importantly, the two-pathway motion computation was implemented as two different image processing flows, one linear (1D or grating motion), one non-linear (2D or features motion). The 1D flow is simply the frame

by frame derivative of the image flow. For the unikinetic plaid, the static grating will therefore vanish and the corresponding 1D cues are the same as for the grating. The 2D flow is obtained by first computing motion energy of the different cues (similar to Weiss et al., 2002), and then applying a mask to remove all information without enough saliency and hence selecting high spatial frequency cues. With the barber pole stimulus, the mask removed most of the motion energy not located along the four edges. With unikinetic plaids, the mask selected the blobs at the intersection between the two gratings. Below, we briefly describe the computational steps and its algorithm. It shall be noticed that we have tried several other implementation of 2D features tracking and obtained similar qualitative and quantitative results in terms of final velocity likelihoods. The key point here is that a single motion computation algorithm was applied to both barber poles and unikinetic plaids.

The 1D flow was computed with a simple derivative kernel in discrete time $K_t = [-1, 1]$ such as $I_{1D} = \langle I_{m,K} | K_t \rangle$ where $I_{m,K}$ is the preprocessed image flow input of *n* frames. The 2D flow was defined first by the energy of high frequencies cues as computed by a kernel K_x similar to a Laplacian operator $I_{energy} = \langle I_{m,K} | K_x \rangle^2$. This operation defines a mask image flow for energies larger than a threshold Θ and which was point-wise multiplied with the squareroot of the energy to obtain a 2D flow: $I_{2D} = (I_{energy} > \theta) \cdot \sqrt{I_{energy}}$.

The Matlab code for our implementation of this step is given below:

I_1d(:,:,2:n_frame)=.5(I_m_K(:,:,2:n_frame) I_m_K(:,:,1:(n_frame-1)));*

end

- % Compute spatial derivative and normalize it deriv=-[1 3 1; 3 -16 3; 1 3 1];% deriv=deriv/sum(deriv(:).^2);
- % spatial blurring blur=ones(3); blur=conv2(blur,blur);blur=conv2(blur,blur); blur=blurlsum(blur(:).^2);

for i_frame=2:n_frame-1,

- % motion energy on high frequencies I_energy=conv2(I_m(:,:,i_frame),deriv,'same').^2; % selection process similar to Weiss et al. (2002) I_mask=double((I_energy>6*std(I_energy(:)))); I_mask=conv2(I_mask,blur,'same'); % combining both
- *I_2d(:,:,i_frame)*=(*I_energy*).^(*1*/2).**I_mask;* end;

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