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Are switches in perception of the Necker cube related to eye position?

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Abstract

The issue of the relation of eye position to perceptual reversals of the ambiguous figure of the 'Necker cube' dates back to Necker's original article [L.A. Necker (1832) *The London & Edinburgh Philosophical Magazine and Journal of Science*, **1**, 329–337]. Despite the investigations of many distinguished psychophysicists since then, the question of whether perceptual switching is a cause or a consequence of associated changes in eye position has remained a matter of debate. In the present study we overcame methodological problems that have bedevilled many previous studies. We avoided any instruction that could interfere with the human subjects' free viewing of the Necker cube, tracked the eye position precisely and used biased versions of the cube that produced unambiguous percepts to determine how each subject actually looked at the cube. We show that, under these free-viewing conditions, there is a close link between the perception of the Necker cube and eye position. The average eye position of most subjects is at an extreme value at about the time when the subject's perception switches. From the biased cube trials we can infer that the polarity of the extreme corresponds to the percept which the subject had before the switch. These data indicate a bidirectional coupling between eye position and perceptual switching so that, after a subject's perceptual state changes, their eye position shifts to view the newly established percept. When the eye position approaches the corresponding extreme, the percept, in turn, becomes more and more likely to switch. This result suggests that the changed eye position itself might provide a negative feedback signal that suppresses the percept.

Introduction

Ambiguous figures produce an alternating perception of the figure, despite constancy in the stimulus. Perhaps the best known ambiguous figure is Necker's eponymous cube, which actually started its life as a rhomboid. Necker, then professor of Mineralology in Geneva, noticed the switch while studying engraved plates of rhomboid-shaped crystals. In a letter to Sir David Brewster in 1832, Necker described the switch which, in his opinion, resulted from 'an involuntary change in the adjustment of the eye for obtaining distinct vision.' Wheatstone (1838) soon showed that Necker's interpretation was wrong on geometric grounds and claimed instead that the switch depended only on 'our mental contemplation'. Wheatstone's interpretation was, of course, strongly influenced by his systematic studies of the related phenomenon of binocular rivalry using his recently devised stereoscope. However, Hering (1879) claimed that the switching rate could be influenced by eye movements and differential retinal adaptation. A century later the debate remains very much alive. Do eye movements relate to perceptual switching or not (Flamm & Bergum, 1977; Ellis & Stark, 1978) and, if they do, do eye movements precede the perceptual switch, as some have suggested (Glen, 1940; Kawabata *et al.*, 1978), or are they an involuntary consequence of the perceptual switch, as others have argued (Zimmer, 1913; Pheiffer *et al.*, 1956)? Unfortunately, most attempts to decide between these options have either had difficulties in accurately measuring the temporal relation of eye position and perceptual switches or had specifically instructed their subjects to make (or to suppress) eye movements. Here we established the temporal relation between perceptual switching and eye position while subjects viewed the Necker cube. Subjects were free to make any eye movement while viewing the cubes, i.e. no instructions regarding eye movements were given.

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Materials and methods

Subjects and stimuli

Eight subjects (25–47 years, four females) participated in the main experiment. Three different conditions were used in all of these subjects: Necker cube trials, biased cube trials and text trials.

Necker cube trials

Necker cubes consisted of white (79.8 cd/m^2) lines (about 0.1° thick) on a black ($< 10^{-3}$ cd/m^2) background. In each of the three Necker cube trials a cube of different angular size (length of edge, 3.8, 7.5 and 11.3° of visual angle) was used. Each Necker cube was presented for 2 min. Subjects were instructed to report their current percept by pressing either button of a two-button mouse. In order not to bias subjects as to which cues to use to determine their percept, the instruction on the association between percept and mouse button avoided verbal instruction. Instead, subjects were shown unambiguous

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(biased) versions of the cube (as described below) and instructed that they should associate each of the versions to one of the mouse buttons. Throughout this work we will refer to the percept with the lower face of the cube in front as 'percept I' and to the other interpretation as 'percept II'.

Biased cube trials

Biased cubes were identical to the Necker cubes, apart from having the perceptually hidden lines drawn in grey (0.71 cd/m^2). By the control experiment described below, we ensured that this evoked one unambiguous percept. In biased cube trials subjects were presented with alternate versions of the biased cube in succession. The stimulus changed from one induced percept to the other on average every 3 s and subjects were asked to 'report the indicated percept'. The distribution of interswitch intervals was drawn from a Gaussian distribution (mean 3 s and SD 1 s) which was cut off at 0.5 and 5.5 s to avoid too fast or excessively long presentation of one biased version. Subjects were instructed to indicate the percept by pressing the appropriate button as in the Necker cube trials. Three biased cube trials preceded (one per cube size) and three biased cube trials followed the Necker cube trials, yielding a total of six biased cube trials.

Text trials

One important issue was to avoid measuring an eye position that was influenced by the means of reporting the percept rather than by the percept itself. Although the standard input device of a two-button mouse that we used for reporting the percept makes such an effect of eye–hand coupling rather unlikely, we chose to control for this potentially confounding issue. As a first and a last experimental trial we asked subjects to press the button of the mouse corresponding to the word ('LEFT' or 'RIGHT' at 79.8 cd/m^2 and about 1°) that appeared alternating on the screen. Alteration between 'LEFT' and 'RIGHT' was performed like the alteration between the biased cube versions in biased cube trials. Any effect which results from the report of the cube percept, but not from the percept as such, would appear in both text and cube trials. Therefore, the text trials are an adequate control for unwanted effects of eye–hand coupling causing eye movements.

A complete experimental session consisted of 11 experimental trials which were conducted in immediate succession: one text trial, three biased cube trials, three Necker cube trials, three biased cube trials and one text trial. In the blocks using cubes (biased or Necker) each cube size was used once and the order of cube sizes was random. Calibration trials for the eyetracking system (described below) were interleaved between experimental trials.

In order to test that the biased cube indeed evoked the intended unambiguous percept, we performed a control experiment in four additional subjects with normal or corrected to normal vision. These subjects were presented with stimuli akin to the biased cubes but in which the luminance values for 'hidden' lines (L_h) were varied. These values included those of the biased cubes of the main experiment ($L_h = 0.71$ cd/m^2), unbiased Necker cubes ($L_h = 79.8$ cd/m^2) and five other values ($L_h = 0$, 0.3, 1, 20 and 40 cd/m^2). Using a Necker cube subjects were instructed on the two possible percepts without reference to the bias. Subjects were asked to report their 'first percept' for each stimulus presentation. After the subject's response, the screen was blanked and the next stimulus was presented after a 0.5-s interval. The combination of each cube size, luminance value and bias direction was presented 20 times to each subject yielding a total of ($3 \times 7 \times 2 \times 20 =$) 840 trials per subject.

Eyetracking

Throughout the experiment eye position was recorded using a non-invasive infrared eye tracker (Dr Bouis, Karlsruhe, Germany; Bach *et al.*, 1983). Stimuli were generated using MATLAB (Mathworks, Natick, MA, USA) including the psychophysics toolbox (Brainard, 1997; Pelli, 1997). The presentation setup, recording setup, fixation of subjects and calibration protocol were as described previously (Einhäuser & König, 2003). In brief, subjects' heads were stabilized with a chin-rest and a bite-bar to minimize head movements. Before each experimental trial, subjects fixated points presented on the screen. From this calibration trial a bilinear coordinate transform was computed in order to map oculometer output voltages to eye position. The fixation grid used for calibration was adjusted to the cube size of the following experimental trial. Consequently, the calibration error also scaled with the cube size. Across trials and subjects the median relative calibration error was 10% of the corresponding cube size. Recording subjects' responses with the same data acquisition card as eye position reduced the relative error between the button-press signal and eye-position signal to below 1 ms. Experiments conformed to national and institutional guidelines for experiments with human subjects and with the declaration of Helsinki. Informed written consent was obtained from all subjects.

Data analysis

From biased cube trials we determined the subject's reaction time from the switch in percept to the button press. As the variation in these reaction times was negligible compared with the subject's interswitch intervals, we could determine the time of perceptual switching by subtracting the subject's mean reaction time from the time of button-press. In order to analyse the eye position relative to this time of perceptual switching, we aligned the eye-position traces at the times of perceptual switching and averaged over these aligned eye traces. In order not to confound the analysis with effects of the preceding or following switch, each eye trace was only used from the time of the previous to the time of the next perceptual switch.

To analyse the dependence of eye position on the perception of the observer, we first aligned all eye traces to the times of perceptual switching. This alignment was performed separately for the switch from percept I to percept II and for the switch from percept II to percept I. We averaged the eye traces within each trial, which resulted in a mean eye trace for each of the two alignments. We then computed the distance between these two mean traces at each time-point. The resulting distance measure (distance over time) as well as its projections on the x- and y-axes (horizontal and vertical distance over time) will serve as a basis for absolute time analysis.

For a first statistical analysis of the distance measure we chose two points of interest: the time of perceptual switching and the absolute maximum of the horizontal distance. At these time-points we assessed, by a t-test, whether the horizontal distance was significant. Vertical distance resulted in qualitatively similar results and is therefore not reported separately.

Optimally, we would like to test whether the distance measure is significant over the whole time series instead of testing at arbitrarily chosen points of interest. As the underlying time series (eye traces) are of different duration (the switch intervals are not constant) this is not possible analytically without normalizing time. Nevertheless, to make a statement on the whole time series in absolute time, we instead used the text trails as baseline. We compared the distance measure time-point by time-point between each cube trial on the one hand and the text trials on the other hand. If eye position in cube trials is indeed dependent on the perceptual state of the observer, the distance measure in cube trials should be larger than in the text trials for most of the time. A conservative estimate of significance is then given by the fraction of subjects for whom the distance is larger in the cube trials than in the text trials for more than 50% of the time. The significance of this fraction was assessed by a sign test. As the mean switch interval was 3 s in biased and text trials, we restricted this analysis to a 3-s interval centred at the time of switching (± 1.5 s).

In addition to the described analysis in absolute time and to facilitate intersubject comparison we also analysed time-normalized eye traces. To achieve independence to the absolute duration of a single percept, the following procedure was applied for each trial. All eye traces for the variable intervals between perceptual switches were normalized to a unit time. The eye traces associated with the same percept were then aligned and averaged. In this normalized time-frame, percept I occupies the first half of the unit interval (0, 0.5), while percept II occupies the second (0.5, 1). Thus, the switch from percept I to percept II occurred at time 0.5, while the switch from II to I occurred at time 1. This representation is referred to as the mean time-normalized eye trace throughout this work. In order to obtain a one-dimensional representation of the time-normalized eye-position data without having to choose an arbitrary axis, a principal component analysis was performed for each trial and the mean time-normalized eye trace was projected on the (long) principal axis. For all Necker and biased cube trials, the sign of the principal axis was inferred from both trials with biased cubes of the same size. The sign was chosen such that the median of the mean normalized eye trace of the biased cube trials was larger for percept I than for percept II when projected on the principal axis. Hence, percept I corresponds to positive values and percept II to negative values.

The procedure described to determine the sign of the principal axis relies on the fact that the medians of the projected mean time-normalized eye traces of the biased cube trials are different in percept I vs. percept II. To assess the significance of this difference we employed a sign test to compare the trace belonging to biased percept I (from time-point 0 to 0.5) with the trace belonging to percept II (from 0.5 to 1) time-point by time-point. As adjacent time-points are not independent of each other, the resulting significance level has to be corrected. In the worst case, the correlation extends over the whole trace. Therefore, an upper bound to the number of dependent samples is the number of sampling points. Performing a Bonferroni correction with this number at the significance level of the uncorrected sign test will provide an upper bound for the true significance level. If this corrected level is still low in most of the trials, the estimation of the sign of the principal axis is justified.

To quantify further the temporal relation between eye position and perceptual switches, one can make use of the fact that, by construction, the mean time-normalized eye traces are periodic and the perceptual switches occur at the fixed time-points 0 (= 1) and 0.5. Therefore, we applied a Fourier expansion to these traces after additionally normalizing the traces to mean 0 and SD 1. The phase of the F1 component provides a measure of the relative timing between the eye position and perception.

Results

We recorded the eye position of eight subjects during free viewing of a Necker cube. Subjects reported the perceptual state of the Necker cube by button presses, so allowing us to assess the temporal relation between perceptual switches and changes in eye position. For comparison, we also recorded the eye position when subjects viewed a Necker cube in which one face was emphasized by bold lines ('biased cubes') or viewed text instructions ('LEFT'/'RIGHT'). Reaction times measured in the biased cube trials were used to correct the measured time of perceptual switching in Necker cube trials. As the variance in an individual's reaction time was negligible compared with the intervals between perceptual switches (the SD of reaction times was at least 11 times smaller than the mean interswitch interval in all subjects), the time of the switch could be determined precisely. We found that there were large variations in the interval between perceptual switches both within each subject and between subjects. The switch intervals were not normally distributed but compatible with a gamma distribution ($P > 0.46$, KS test), as has also been observed previously (Borsellino *et al.*, 1972). As explained below, the large variations in the interswitch interval distribution impose difficulties on obtaining quantitative results from eye traces averaged in an absolute time-frame.

Analysis in an absolute time-frame

In Fig. 1a we show an eye trace of an individual subject (RS) while viewing the large (11.3°) Necker cube. While there is no obvious single eye movement that could readily be associated with perceptual switching, 300 ms after the switching there is a clear separation of eye positions according to the polarity of the switch (Fig. 1b). How does this separation vary depending on the temporal distance to the switch? To address this issue we first aligned the eye traces to the perceptual switches and found that RS's switch from percept I to II occurred while his average horizontal eye position was at its rightmost location (Fig. 1c) and that the reverse switch occurred while the eye position was at its leftmost location (Fig. 1d). The vertical eye position showed a similar pattern by being at its topmost location at the switch from I to II and at its bottommost location at the reverse switch (data not shown). The example subject RS consequently showed a clear separation of eye position depending on the polarity of the switch. His mean eye position took its extreme values at about the time of his perceptual switches. The difference between eye positions (Fig. 1e) was indeed highly significantly different for the two switch polarities at the time of switching ($P < 10^{-6}$, *t*-test).

Next we investigated whether this behaviour was conserved across trials and subjects. For simplicity we only show the horizontal eye position but the vertical eye position yielded qualitatively similar results with respect to timing. Our example subject, RS, behaved consistently across all three Necker cube trials (Fig. 2a, seventh column). At the time of switching, RS's eye position was significantly dependent on the switch polarity for all cube sizes ($P < 10^{-3}$, *t*-test for any cube size); this was also true for AS ($P < 0.02$ in any cube size). The consistency across cube sizes was true for most subjects, who showed a strong modulation of eye position relative to the perceptual switching (Fig. 2a). However, there were clear qualitative differences between subjects; while, like RS, AS's eye positions were at their extremes at times of perceptual switching, for PB they were about half-way in between (Fig. 2a, fifth column). Therefore, when testing at the time of switching, of all of the subjects only AS and RS showed a significant effect for all cube sizes. Consequently, we then analysed the distance of each individual's eye position around the switch from percept I to percept II to the eye position at the equivalent time-point around the switch from percept II to percept I (Fig. 1e). The time when this distance reached its maximum was widely distributed (Table 1, t_{peak}). However, at these times the difference was significant in all but three of the 24 Necker trials (Table 1, P_{peak}). In order to rule out the possibility that this effect arose from methodological or

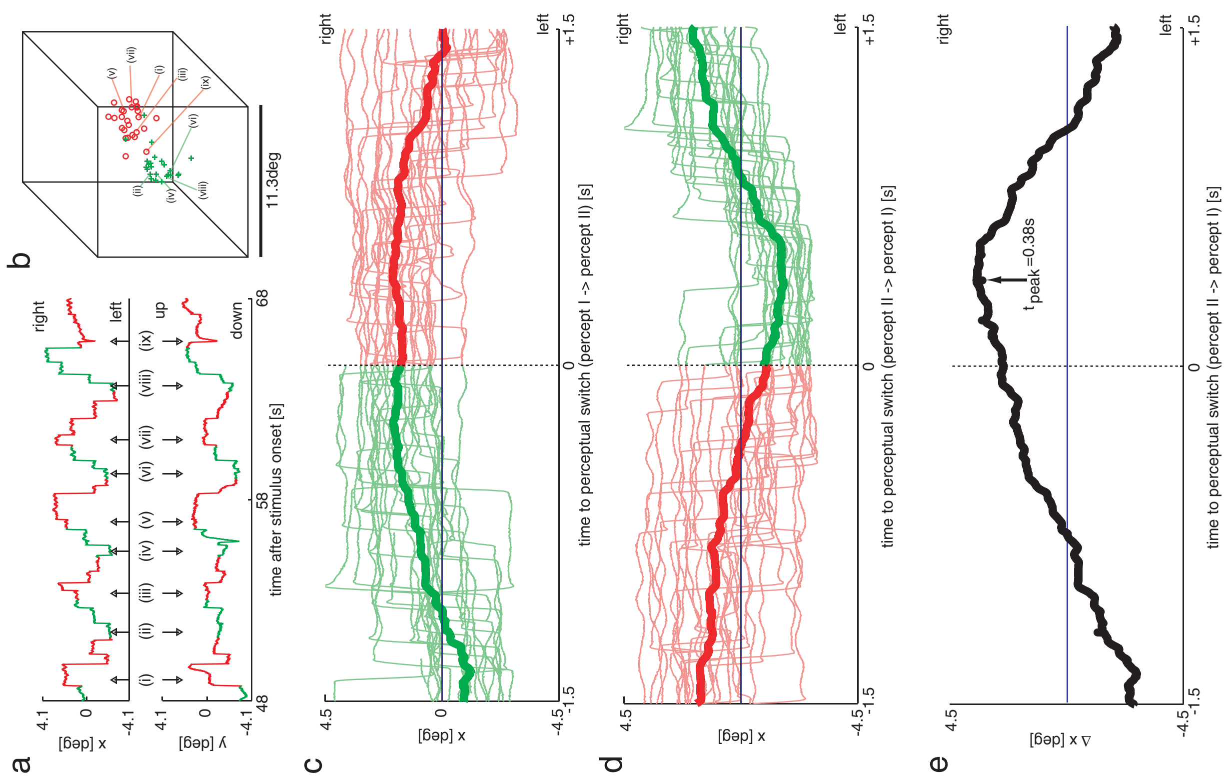

FIG. 1.

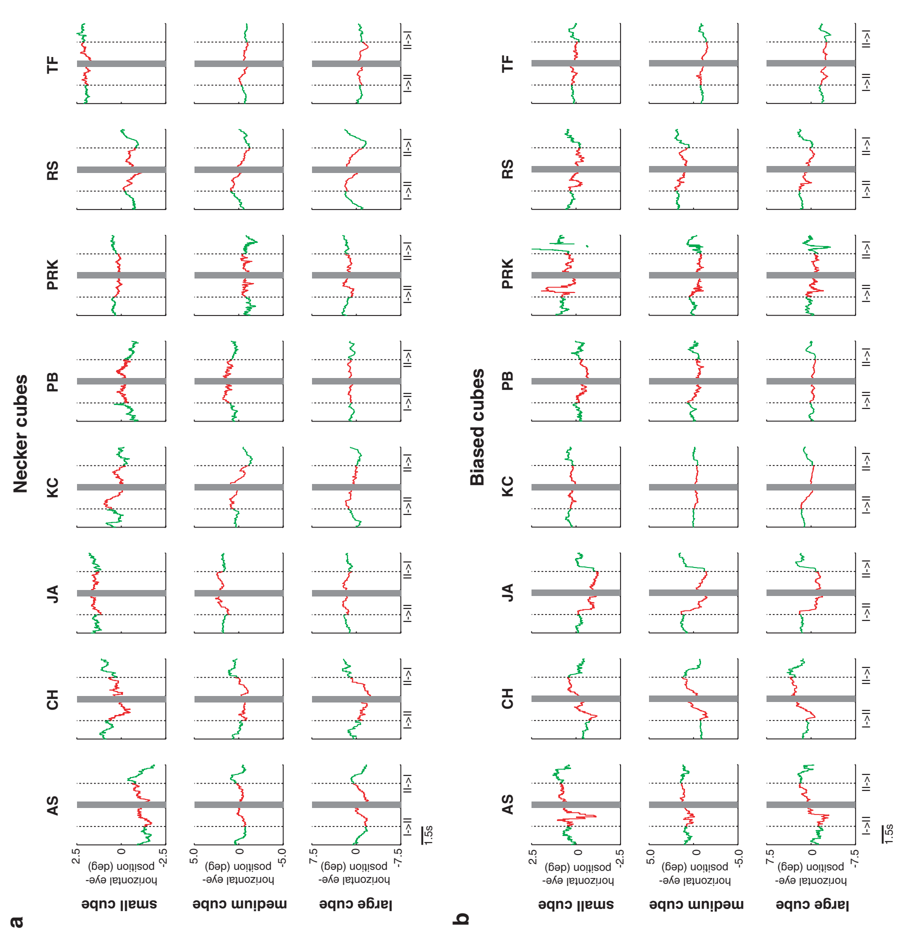

FIG. 2.

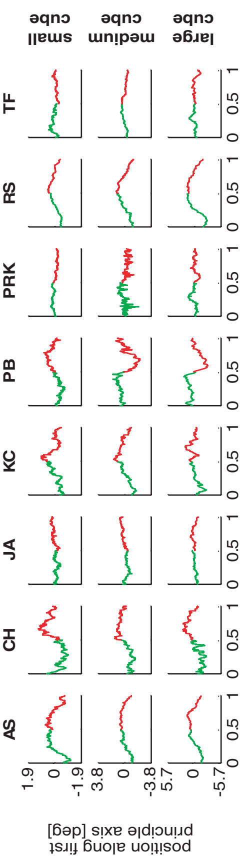

FIG. 3.

TABLE 1. Absolute time analysis

Subject	Small cube t_{peak} (s)	Small cube P_{peak}	Small cube Necker > text*	Medium cube t_{peak} (s)	Medium cube P_{peak}	Medium cube Necker > text*	Large cube t_{peak} (s)	Large cube P_{peak}	Large cube Necker > text*
AS	+0.24	0.000007	94.9	+0.33	$< 10^{-6}$	97.7	−1.39	0.00001	100.0
CH	+0.66	0.0008	95.6	−1.26	0.004	95.5	+1.36	0.000007	99.8
JA	−1.24	0.102	83.7	−0.11	0.066	96.1	−1.23	0.037	96.6
KC	+0.56	0.0007	100.0	+0.21	0.0001	99.9	+0.54	0.0006	100.0
PB	−1.05	0.003	98.7	+0.54	0.000004	99.3	+0.69	0.011	99.5
PRK	+1.01	0.00009	68.9	+1.00	0.023	81.6	+0.67	0.082	87.5
RS	+1.50	0.00002	87.7	+0.13	$< 10^{-6}$	92.5	+0.38	$< 10^{-6}$	100.0
TF	+0.69	0.009	87.5	+0.56	0.001	98.2	−0.35	0.021	92.6

All analysis is based on the differences of the mean over eye traces aligned to the switch from percept I to II vs. the mean over traces aligned to the switch of opposite polarity (II to I). For each subject and cube size t_{peak} is the time when the maximum absolute difference in horizontal eye position is reached relative to the time of the perceptual switches. P_{peak} is the significance (*t*-test, uncorrected) of this difference at the time-point of t_{peak}. *Necker > text uses the Euclidian distance between the mean traces in the Necker cube trials and compares it time-point by time-point with the same measure in the text trials. This ratio is expressed as the percentage of time when the distance is larger in the Necker trial than in the text trial (chance level is 50%).

statistical artifacts we directly compared the time-course of the distance to the same measure for the text trials. We analysed the 1.5 s before and after the switch. For any of the 24 trials, the distance was larger for Necker cubes than for the text stimulus at least 68% of the time (Table 1, Necker > text). Even this worst-case number was far above the chance level of 50% and the mean over all trials amounted to 90%. This shows that the difference in eye position observed between the two percepts was not only significant at the peak but also nearly always larger compared with control. Ignoring the large difference from chance level and considering just subjects but not trials as independent provided the most conservative estimate for significance: observing above-chance performance in eight of eight subjects then corresponded to $P = 0.008$ (sign test) but, if we considered trials as independent, this level dropped to $P = 1.2 \times 10^{-7}$. As the text trials required the same type of physical response (button press), this analysis rules out the possibility that the observed relation for the cubes could be a mere consequence of the button press used to indicate the percept or any other setup artifact. In conclusion, eye position clearly depended on the perceptual state. However, a clear temporal relation of switching and eye position cannot be established in an absolute time-frame. We consider this to be the consequence of the high variability of interswitch intervals within and across trials. This problem is enhanced by the gamma distribution of interswitch intervals, as there are comparably more very short and very long interswitch intervals than there would be for Gaussian distribution of the same variance. Consequently, we will also analyse the temporal relation of switching to eye position in a normalized time-frame.

Not only did the timing of eye position relative to perceptual switches differ but so did its polarity. This difference was most visible by comparing subjects AS and RS, whose eye positions both took their extreme values around the time of perceptual switching. While RS was consistently at the rightmost extreme when switching from percept I to II and at the leftmost when switching from percept II to I, AS showed exactly the opposite behaviour. Does this effect reflect a difference in the timing of the eye position relative to the perceptual

FIG. 1. Example subject. (a) Excerpt of the eye position (top, horizontal; bottom, vertical) of an individual subject (RS) while viewing a Necker cube whose faces span 11.3° of visual angle. Green indicates that the subject perceives percept I (lower face in front) and red percept II (right face in front). Timing of perceptual switches is corrected for reaction times. The centre of the screen (0°) was also the centre of the cube. Positive values correspond to right and up and negative values to left and down. (b) Eye positions are relative to the stimulus, 300 ms after the times of perceptual switches (cube size 11.3°). Data are taken over the whole trial, from which the example eye trace in (a) is taken. Roman numerals indicate corresponding points between (a) and (b). (c) The horizontal eye position of the example Necker cube trial aligned to the time of perceptual switching (at $t = 0$) from percept I (faint green traces) to II (faint red traces). Each eye trace is used only from or up to the time of the next perceptual switch. Missing data within a trace result from blinking. Thick red and green lines indicate the average over the aligned eye traces. As above, positive values correspond to right and negative to left. (d) Analogue to (c), traces aligned to switch from percept II to I. Note that in both (c) and (d) the average eye position takes its extreme value around the time of perceptual switching. (e) Difference between mean traces of (c) and (d). Maximum is marked by arrow.

FIG. 2. Relation of percept and eye position for all individuals in an un-normalized time-frame. Horizontal eye traces are temporally aligned to the time of perceptual switching and averaged. In each panel ordinates indicate eye position in screen coordinates and abscissae absolute time. The dashed line on the left-hand side of each panel indicates the switch from percept I to percept II and vice versa on the right. Green always indicates percept I and red percept II. As interswitch intervals vary within and across subjects, in this absolute time-frame the left-hand side of each plot cannot be connected with the right-hand side to one single time axis; this discontinuity is indicated by the shaded area. (a) Result for all unbiased (Necker) cube trials, columns correspond to subjects, rows to cube sizes and *y*-axes are scaled accordingly. (b) Result for all biased cube trials; within each subject the average is taken over both biased cube trials of the same cube size (before and after Necker cube experiment), rows, columns and scaling as in (a).

FIG. 3. Relation of percept and eye position for all individuals in a normalized time-frame. Mean of projections of time-normalized eye traces on the principal axis for all subjects and all Necker cube trials. Rows correspond to cube sizes (increasing from top to bottom) and columns to subjects. Note that the panel's vertical axes are scaled according to cube size. The vertical axis shows the eye position along the first principal axis. The sign of the axis is determined by the bias of the eye positions as measured in the biased cube trials in the same subject and cube size; positive values correspond to biased percept I and negative to biased percept II. As in Fig. 2, the two trace colours indicate the two percepts as reported by the subjects (green, I; red, II). By construction the switch from percept I to percept II happens at time-point 0.5 and the switch from II to I at time-point 0, which is identical to time-point 1 in the periodic time-frame.

switching or does it result from selecting different features of the cube to judge its orientation? When asked after the experiment, both subjects indeed reported that they tended to select a particular feature: AS reported using the cubes' faces for reference, while RS selected the corners. Using the biased cube trials, we can infer the differences between subjects in cues selected without having to rely on their subjective reports. Indeed, AS showed a bias towards the (lower) left when perceiving percept I (lower face in front) and a bias to the (upper) right when perceiving percept II, while the opposite was true for RS (Fig. 2b). However, it is also clear from Fig. 2b that, for most subjects, this difference only represented a bias towards one or the other eye position when averaged over the whole interval while one biased percept is shown, while only a few subjects promptly adjusted their eye position and kept it (on average) stable thereafter (as best seen in JA, Fig. 2b, third column). Nevertheless, the dependence of eye position on (induced) percept was nearly as strong as in the Necker trials (mean, 84% of time larger than text control; minimum over all trials, 56%; $P = 0.008$, sign test as in Necker trials). In addition, the observed bias was very consistent with the subjects' subjective report. AS and CH reported using the faces, while all other subjects selected corners. For AS and CH all biased cube sizes showed a bias to the left for percept I and a bias to the right for percept II, whereas all other subjects showed the opposite behaviour for all biased cube sizes.

In order to ensure that the biased cube trials were an adequate baseline for the Necker cube trials we presented biased cubes of different bias strength to a new group of subjects. We asked subjects to indicate their 'first percept' when a cube was presented. The effectiveness of the bias depends on the luminance of the 'hidden' lines. When the luminance of the 'hidden' lines was half (40 cd/m^2) that of the 'visible' lines, the bias was only effective in 64% (SD 11%) of the cases (mean over subjects and cube sizes). The effectiveness increased monotonically for further luminance reduction [20 cd/m^2, 77% (SD 12%); 10 cd/m^2, 84% (10%); 1 cd/m^2, 95% (4%); 0.7 cd/m^2, 95% (4%); 0.3 cd/m^2, 96% (2%); 0.0 cd/m^2, 98% (1%)]. The minimum effectiveness of the bias across all tested subjects for the luminance level used in the main experiment (0.7 cd/m^2) was 90%. We conclude that subjects perceived the biased cubes in the main experiment as intended. This justifies the use of the biased cube trials to determine the sign for Necker cube trials in the analysis described below.

To facilitate intersubject comparison we performed the time-normalized analysis in a one-dimensional frame of reference. Principal component analysis indicated that the eye positions varied mainly along an axis that lay approximately parallel to the main diagonal (lower left to upper right) of the cube. For Necker cube trials 11 of 24 fell within 10° of this main diagonal and 20 of 24 within 30° around the main diagonal. Across all subjects, the principal axis explained more than 75% of the variance of eye positions for most Necker cube trials (19 of 24). In the case of biased cubes this fraction was smaller (31 of 48), indicating that subjects deviated from the main axis more than in the Necker cube trials. Nevertheless, the main diagonal was still the predominant axis (31 of 48 trials within 30°, while chance for homogeneously distributed preferred axes would only predict 16 of 48), indicating that the strategies employed for biased and Necker cubes were similar. On the other hand, in only half (eight of 16) of the text trials did the principal axis explain more than 75% of the variance and its direction was close to chance (0 of 12 within 10° and five of 12 within 30° of main diagonal; chance levels, 1.3 of 12 and four of 12, respectively). This indicates that there is a strongly preferred axis which is related to the perception of the cubes. Hence, performing intersubject comparision in a one-dimensional frame of reference along the principal axis is justified.

The sign of each principal axis was chosen such that the median of the projected mean time-normalized eye trace of the corresponding biased cube trial was larger for percept I than for percept II. This assumes that these medians are different. Using the Bonferroni-corrected paired sign test (see Materials and methods) 83 of the total of 88 (24 Necker cubes, 48 biased cubes and 16 text) trials indeed showed a significant difference in the median. (The exceptions were the first text trial in CH, first large biased cube trial in AS and TF, medium Necker cube in PB and large Necker cube in AS.) Given that this test provided an upper bound on the significance levels, while the actual significance levels may well be much smaller, we used cubes to determine the sign of the principal axis in all trials. We thus can confidently associate percept I with positive values and percept II with negative values along the principal axis in all trials.

The similar principal axis and the similar eye position modulation strength for biased and Necker cubes as well as subjective reports provide clear evidence that the biased cubes are an adequate baseline for the Necker cubes. Nevertheless, it cannot be ruled out that different factors, such as two-dimensional luminance distribution, may differentially affect eye position in Necker and biased cube trials. Hence, it is important to note that the assignment of signs achieved on the basis of biased cube trials was fully consistent with that achieved on the basis on the subjects' reports.

Analysis in a normalized time-frame

For further quantification of our results we then used the time-normalized eye trace along the principal axis, whose sign was determined from the biased cube trials of the same cube size. Figure 3 shows the resulting representation of our data. This time-normalized representation reveals that most subjects' eye positions exhibited a strong modulation with a fixed phase relative to their perceptual switches. The amplitude of the eye positions for most subjects depended on the size of the Necker cube but the phase relative to the perceptual switches was consistent across cube sizes for most subjects. One exception was PB, whose pattern reversed for the smallest cube size. Note that in this representation AS and RS, for example, exhibited the same patterns, as expected from the discussion of the un-normalized data.

By making use of the fact that this time-normalized representation was periodic in time, we then compared subjects quantitatively by performing a Fourier analysis of the data and investigating the F1 component. Figure 4a illustrates how the different idealized mean normalized eye traces of Fig. 3 would translate into Fourier space: The relative timing of perceptual switching to eye position is reflected in the F1 phase. The phase of the mean F1 component in Necker cube trials (grey arrow in Fig. 4b) is −114°. This implies that, on average, eye position takes its extreme values around the times of perceptual switching (see scheme in Fig. 4a). While the trials of subjects AS and RS were found to be close to this mean value, justifying their use as typical examples, the deviating behaviour of PB, also described qualitatively above, was reflected by the proximity of its F1 components to the real axis (Fig. 4b, diamonds). Not only did the mean F1 component show a negative imaginary part (i.e. a phase between −180° and 0°) but so did most (19 of 24) individual trials. This result goes beyond the finding that perceptual switching occurred on average at extreme eye positions (which would also be consistent with a phase of about +90°); the polarity of the extreme at a given perceptual switch was consistent with the percept before that switch.

We performed the same analysis for the biased cube trials and the text trials. In the biased cube trials the percept was externally triggered

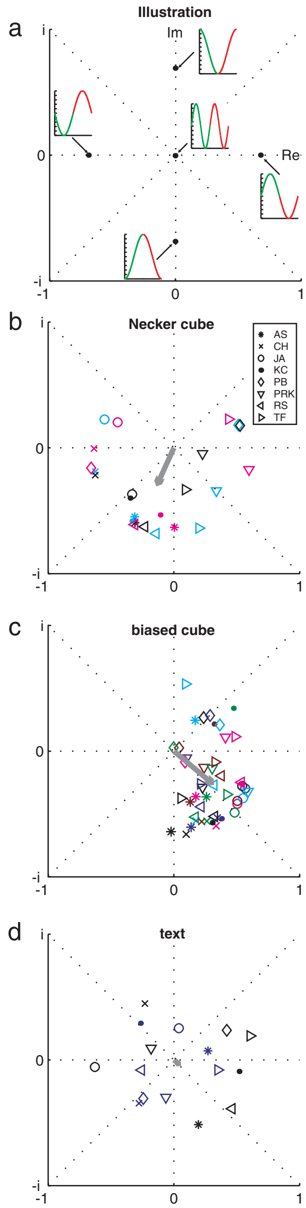

FIG. 4. Complex plane representation of the first Fourier (F1) component of all projected time-normalized eye traces. (a) Idealized examples of eye traces according to the representation of Fig. 3 and how they would translate into the F1 representation used in this figure. (b) F1 component of all time-normalized eye traces of Fig. 3 (Necker cubes); symbols identify subjects as shown and colours cube sizes (magenta, small; cyan, medium; black, large). Grey arrow indicates mean F1 component $<F1>$. (c) F1 component of all time-normalized eye traces of biased cube trials; symbols identify subjects as in (b) and colours cube sizes and time of trial (before/after Necker cube trials) (magenta, small cube before; cyan, medium cube before; black, large cube before; red, small cube after; green, medium cube after; blue, large cube after). (d) F1 component of all time-normalized eye traces of text trials; symbols identify subjects as in (b) and colours time of trial [before (black)/after (blue) biased and Necker cube trials].

by a change in the stimulus. If a subject's eye position responded perfectly consistently and without any delay to the change in percept one would expect a F1 phase of 0°. On average, the eye position lagged slightly behind (phase of mean, −40°) and most individual trials (36 of 48) fell between 0° and −90° (Fig. 4c). This shows that eye position consistently followed the induced change in percept.

We used the text trials as a baseline for the analysis and especially to rule out any setup-related effects, such as of the subject's manual response, on eye position. As the eye traces were normalized to unit variance before the Fourier transform, the amplitude of the mean F1 component was a measure for distribution of the phase across trials. This amplitude of the mean F1 component was more than five times larger in the Necker ($(|<F1>| = 0.31)$ and biased ($|<F1>| = 0.37$) cube trials than in the text trials ($|<F1>| = 0.06$, Fig. 4d). This shows that the phase in the cube trials was more consistent across subjects than in the control (text trials). Consequently, although the phase of individual subjects had a considerable spread around the mean in the cube trials, the behaviour of an individual was still more consistent with the population mean than expected by chance.

Discussion

We measured the temporal relation of eye position to perceptual switches in the appearance of a Necker cube. Unprompted, subjects' perceptual switches were consistently associated with different eye positions, regardless of the particular features of the Necker cube which an individual subject chooses to foveate. This relationship is remarkable given that the target itself has not shifted but only the perception of its three-dimensional geometry.

This result throws new light on a longstanding debate which was begun by some of the most eminent scientists of the 19th century. They divided into two camps on the issue of whether the perceptual switch reported by Necker was 'mental' or whether it was driven by a reflexive 'involuntary' motor act. Necker (1832), Brewster (1847) and Hering (1879) were nativists who interpreted sensations as a true account of the material world. For them, the 'involuntary' eye movements produced a changed sensation that caused the perceptual switch. On the other side Wheatstone (1838), von Helmholtz (1867) and Wundt (1897) were empiricists, for whom sensations provided only signs that had to be interpreted, often unconsciously, through our prior experience of the world. Hence Wheatstone's opinion that the switches were the results of 'mental contemplation'.

In one of the most detailed studies on the relation of eye movements to the percept of the Necker cube, Glen (1940) found a clear correlation between eye movements and reversal. When subjects were instructed to make switches happen 'as rapidly as possible', Glen's data suggest that eye movements slightly precede the perceptual switch. These results directly challenged the earlier observation of Zimmer (1913) that eye movements do follow perceptual switching. However, Glen thought that his analysis indicated that the eye movements occurring after the perceptual switch 'had become associated with whatever type of objective response is adopted for reporting perceived reversions. The random phase found for the text control in our study, however, excludes such an association between response and eye position as one possible interpretation. In his 'spontaneous observation' task, which corresponds most closely to our experimental condition, Glen could only state the 'close proximity' of eye movements and time of perceptual switching, without a clear statement of causal direction.

Using a rather crude method to mark perceptual switches, Pheiffer *et al.* (1956) again supported the result of Zimmer (1913) and argued in favour of perceptual changes leading to eye movements and not vice versa. Their results had, in turn, been challenged on technical grounds by Flamm & Bergum (1977) who found no significance difference in the number of eye movements in a 1-s interval around the perceptual switch compared with other intervals. However, they instructed their subjects ‘not to be concerned if no switch occurred’, which might bias subjects to fail to report a switch. Such failures to report a switch would confound their ‘control’ intervals, which were assumed to be free of perceptual switches. Furthermore, as Flamm & Bergum (1977) did not measure the magnitude of the eye movements, their observation that there is no relation between perceptual switches and the number of eye movements does not rule out a relation between perceptual switches and eye position.

The issue of eye position rather than saccade frequency or direction was also addressed by Ellis & Stark (1978). From data taken from a single subject at the instance of the perceptual switch they found a clear clustering of eye positions that depended on the polarity of the switch, as observed in the present study. However, unlike the present study, Ellis & Stark (1978) did not try to address explicitly the question of the relative timing of eye position change and perceptual switching. Ellis & Stark (1978) reported prolonged fixation times around the instant of perceptual reversal. Their result could not be replicated by Ito *et al.* (2003) who interpreted it as an artifact of a sampling bias known as the ‘bus paradox’. Here long fixations would be more likely to contain an independent random event (the perceptual switch) than shorter fixations.

Kawabata *et al.* (1978) used a clever technique from which they inferred that eye position causes the percept and not vice versa. They made subjects fixate different corners of the Necker cube and found that subjects significantly favour the interpretation that the fixated corner belonged to the frontal part of the figures. However, corners are clearly a no more ‘natural’ cue for the Necker cube than edges or faces. In fact, in the present study we avoided biasing the subject as to what feature or cue to use. Using the biased cube trials (which are consistent with the subjective reports) as reference, we found that some subjects use the inner corners instead of the cube’s faces or outer corners. This would yield seemingly inverted eye position patterns, which would lead to an incorrect interpretation if one had relied only on the Necker cube data and wrongly assumed that all subjects use the faces or outer corners as cues. Furthermore, it is not clear that the instruction to fixate does not interfere with the subject’s report, especially as Glen (1940) reported a dramatic dependence of switching rates on fixation instructions. Hence, providing explicit fixation instructions, especially in combination with instructions to facilitate or inhibit switching percepts (Peterson & Hochberg, 1983), is unlikely to produce results that are valid for free, spontaneous viewing.

As an interesting corollary, Leopold *et al.* (2002) showed that perceptual switching depends on the continuous presence of the percept; if the percept is interrupted, e.g. by periodically removing the stimulus for some seconds, one particular view of the Necker cube can be stabilized. This implies that a memory of the percept persists, suggesting that the persistent activity of ‘working memory’ neurones in parietal or prefrontal cortex may be involved. As the same regions are associated with the planning and control of saccadic eye movements, the close link between eye position and switches in the percept of the Necker cube might point to a common neuronal substrate.

In summary, most evidence in favour of eye movements causing perceptual switches was indirect, using switching rates and effects of different instructions as a main line of argument. On the other hand, most studies arguing in favour of the opposite causal relation had been bedevilled by technical or conceptual problems. Our results may reconcile both views. In free-viewing conditions we find a tight link between switches in perception and eye position. Our phase analysis indicates that this link is bidirectional; after perceptual switching eye position on average changes towards a location consistent with the newly established percept. At the time that the eye position is most consistent with this percept, the switch back to the other percept occurs. One simple interpretation of these data is that the eye position provides a feedback signal which suppresses the current percept. By this negative feedback mechanism voluntary eye movements or deliberate suppression of eye movements can influence perceptual switching rates, while changes in percept can still lead the eye position. The negative feedback hypothesis thus provides an explanation for seemingly conflicting previous results and is consistent with our data. In particular, the interpretation is consistent with the findings of Leopold *et al.* (2002), i.e. interruption of the stimulus might suppress the suggested negative feedback mechanism of eye position on and thus stabilize the current percept. Direct tests of this negative feedback hypothesis are thus likely to provide further insight into the interaction between eye position and the perception of the Necker cube.

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