RESEARCH ARTICLE

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Properties of saccades generated as a choice response

Abstract Since Hick's original description, many subsequent studies have confirmed the logarithmic relationship that exists between response time and the number of alternatives (NA) for a choice response. In the present study a novel paradigm was used to quantify saccade response time as a function of NA. Normal subjects were required to make a saccade to the remembered location of a visual target whose color was specified by a centrally located cue. The paradigm thus required a stimulus-response transformation similar to that used by Hick. The results show that, when such a transformation was required, a logarithmic relationship was found for saccadic response time. The use of a color-to-location paradigm to study saccade choice response time produced an unexpected additional result that may provide insight into the neural organization of the saccadic system. When the number of alternative choice responses was large (4 or 8), subjects frequently made a two-saccade response instead of a single saccade to the correct location. The first movement in such a sequence was in the correct direction, but was hypometric. A second movement then followed which moved the eyes onto the correct location. These results suggest dynamic dissociations in the mechanisms underlying the triggering of saccades and the specification of their metrics.

Keywords Choice decision · Hick's law · Number of alternatives · Response time · Saccade

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Introduction

Saccadic eye movements can be generated either reflexively or in a more cognitively controlled manner based on the demand of the cognitive task at hand. In the former situation, a visually guided saccade is directed to a target determined by the saliency of the target. In a typical realization of the latter situation a target is selected out of a number of alternatives in the scene that are more or less equally salient, and the saccade is cognitively guided because the response is generated based on processing of perceptual information but not by perceptual saliency itself. In this sense, cognitively guided saccades are a choice response (Luce 1986), as opposed to a simple reaction to a visual stimulus as is the case in visually guided saccades.

Hick's law describes the relationship between response time and the number of alternatives (NA) in making a choice response (Hick 1952; Hyman 1953), and the relationship has attracted much attention from psychologists and theoretical cognitive scientists because the logarithmic relationship of the law defies simple intuitive explanations (Laming 1968; Luce 1986). While a number of models that may account for the relationship have been proposed (Christie and Luce 1956; Laming 1966; Pachella 1974; Teichner and Krebs 1974; Usher et al. 2002), recently a claim has been made that the law is not obeyed by the saccade system (Kveraga et al. 2002). In the pro-saccade task of their experiment, the latter authors used a semicircular array of potential target locations. Subjects fixated a central disk of light and when it was turned off, one of the peripheral stimuli that was the target for a saccade appeared. The number of potential targets varied from one to eight, but was kept constant within a block of trials. They found that saccade latency did not change significantly as a function of the number of targets.

This claim led to a corollary that the brain mechanisms for saccadic target selection are unique and work differently than those for other types of choice behavior. If this were true, then many previous studies (Schall 2001 for a review) that used saccades as a response modality of

higher cognitive functions would be quite limited in terms of their generalizability. However, the paradigm used in the study claiming an exception for saccades was not a choice response task similar to that used by Hick and others. In Hick's work, a particular key on a keyboard was associated with the location of a particular visual stimulus, requiring a transformation of the location of a stimulus in visual space into a choice response of a particular key on the keyboard, i.e., a stimulus-response translation, and response time (the time when the key was pressed) was measured in blocks of trials with different numbers of choices. In the pro-saccadic paradigm of Kveraga et al. (2002) the response instead could result from a more direct linkage from a visual stimulus to a motor response in similar spatial coordinates, as found in the superior colliculus, so the need for stimulus-response translation was minimal. The exceptional finding for saccades therefore is consistent with previous observations (Leonard 1959; Morin and Forrin 1962; Welford 1968; Heywood and Churcher 1980) that simple pointing tasks in general do not obey the law because they do not require stimulus-response translation, which is the major determinant of the logarithmic relationship between response time and NA (Fitts and Posner 1967; Welford 1968; Teichner and Krebs 1974). In fact, a logarithmic increase of response time with NA, i.e., Hick's law, was observed in the same study by Kveraga et al. (2002), when the task was an anti-saccade task in which a response was not in register with, but opposite to a stimulus and thus a stimulus-response translation was required.

Therefore, we began our experiments by re-testing to see whether the saccade system violates Hick's law when a more typical choice response task is used. While conducting the experiment, we found that saccadic responses were frequently made in two-saccade responses, rather than in a single jump, especially in situations where it took a long time to form a choice decision. We believe this unexpected observation shows that triggering a saccade and specifying metrics of the saccade proceed in parallel and can sometimes be dissociated.
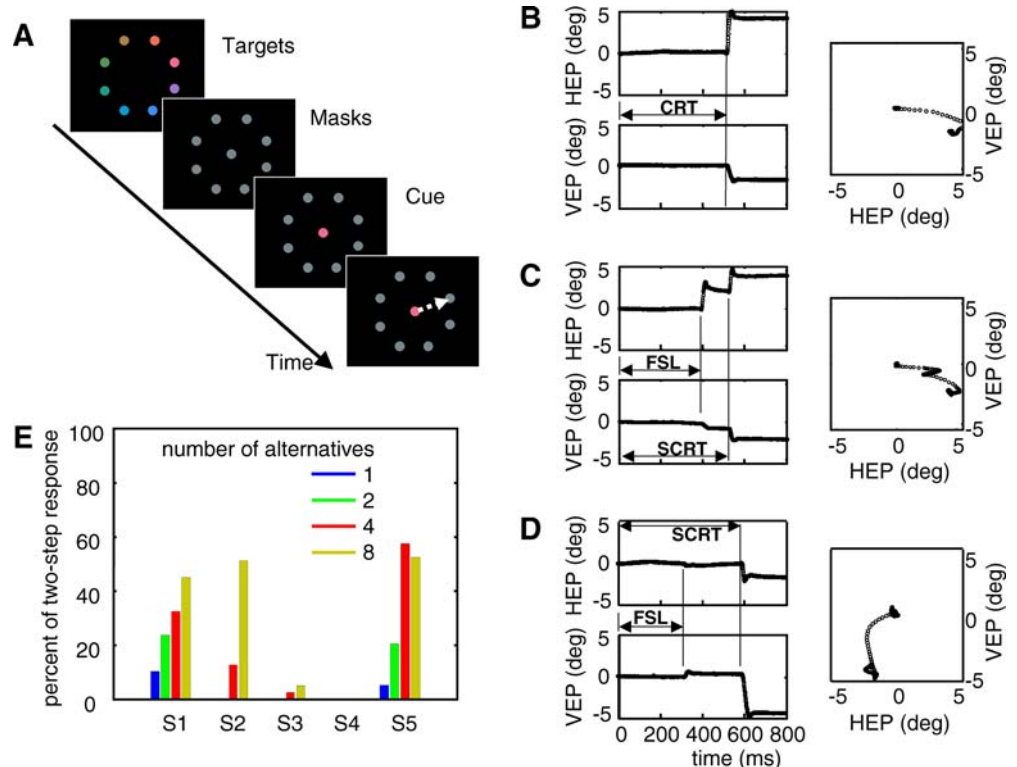
Methods

Experiments were conducted according to a protocol approved by the Institutional Review Board at the California Pacific Medical Center. Five subjects (age range: 24–45 years old) participated after giving an informed consent. They were naïve to the purpose of the experiment, had normal visual acuity and color vision, and reported no history of neurological disorders.

Behavioral task

Subjects performed a cued choice task in which the required saccade target location was specified by a color cue given at the fixation point (Fig. 1a). The number of alternative targets in the array, i.e., the number of color-location associations to be used for a trial, was varied across blocks but was fixed within a block to be 1, 2, 4, or 8. The color-location associations were kept constant throughout an individual experiment. For the 1-NA condition, only the green target located at an eccentricity

Fig. 1 a The sequence of events in a trial of the color-location association task. The figure illustrates the 8-NA condition. See the text for details concerning the paradigm. b–d Eye traces are shown for examples of a single-saccade response (b) and two-saccade responses (c and d). In each figure, the top-left pane is a horizontal eye position (HEP)-time plot, the bottom-left a vertical eye position (VEP)-time plot, and the right panel a HEP-VEP plot. The target was located at 5 deg from the center and at 15 deg down from the right horizontal meridian for b and c, and at 15 deg to the left from the vertical meridian for d. All examples were from 8-NA condition. For definitions of CRT, FSL, SCRT, see the text. e The proportion of trials with a two-saccade response among all correct trials is plotted for each NA and subject (S1–S5)

of 5° and in a direction of 15° above the left horizontal meridian was shown. For the 2-NA condition, either the green or violet target (the colored disk opposite the green) was shown. For the 4-NA condition, one of the set of four colored disks separated by 90 deg, including the green and violet, was shown. Each block consisted of 20 trials. Each subject ran one, two, four, and eight blocks for NAs of 1, 2, 4, and 8, respectively. This scheme ensured that the same number of trials with the green target and cue were collected for each NA condition. The order of blocks with different NA was randomized across subjects.

Subjects were encouraged to memorize the fixed location of the colors in the array before a recording session started. Practice trials were given until subjects were confident they could do the task and the correct performance was observed above 80% in ten successive trials with eight alternatives. When the recorded trials began, the subjects centered their gaze near the center of the screen and pushed a button when they were ready. The button push triggered the display of the color array and started a trial. The target array was displayed for 1,000 ms to remind subjects of the color-location associations and the NA for the trial. The targets were then replaced by gray masks at the same time as a spot of the same gray color appeared in the center of the array to serve as a fixation spot. After a random fixation period (600 to 1,200 ms), the fixation spot turned into one of the target colors. Subjects detected the color-change of the fixation spot as the cue to generate a saccade. They were instructed to saccade to the remembered location of the cued target as fast and accurately as possible.

A color monitor (NANAO FlexScan T2–17, Eizo Nanao Co., Ishikawa, Japan) was used for display of visual stimuli, positioned in front of the subject at 75-cm distance. The targets and masks were half-degree-radius disks that were located on an imaginary circumference at 5 deg of eccentricity. The target colors were chosen by the following criteria: 1) they were isoluminant with each other and with the gray disk shown as the fixation spot and at the target locations as masks; 2) the distance in CIE 1976 (L*a*b*) space, which is approximately uniform in perception of color difference (Wyszecki and Stiles 1982), was the same between each pair of neighboring two colors and between each color and the gray fixation spot. A chromameter (CS-100, Minolta Photo Imaging USA, Mahwah, NJ) was used for measuring luminance and chromaticity of the target colors.

Eye movement recording

While subjects performed the color-location association task, eye movements were monitored by a dual-Purkinje-image eye-tracker (Crane and Steele 1985) (SRI International, Menlo Park, CA) at a sampling rate of 1,000 Hz. Display of visual stimuli was controlled by a Macintosh computer, which was interfaced with a PC that collected and stored the eye movement data. Saccades were detected off-line based on the velocity profile of the eye traces (velocity threshold: 30°/s) by an automated algorithm followed by visual confirmation. No saccades with response times less than 100 ms or more than 1,100 ms occurred.

Figure 1b–d shows sample saccadic responses and the time-intervals defined for analysis. The pair of traces in Fig. 1b shows a single-saccade response that went directly to the correct target. Responses times were measured from the cue onset (zero on the time scale). We call the onset time of these single-saccade responses a choice response time (CRT). The trajectories and end-point dynamics of saccades measured with the dual-Purkinje-image eye-tracker are not accurate, but the final steady-state eye positions are accurate (Deubel and Bridgeman 1995). Specifically, the hooked final trajectories of the sample saccades shown in Fig. 1b–d are an artifact of the tracker.

The traces shown in Fig. 1c are an example of two-saccade responses, which will be described in detail below. Since Hick studied button presses as the response to choice, it is unclear which point in time on the two-saccade responses should be used to allow comparisons to be made to Hick's conclusions. Perhaps the end of the second saccade, when the eyes reached the target, would be the measurement that corresponds most closely to that in previous studies using manual responses in which the time to manually reach a target was recorded. Since the end times of saccades are not accurately measured with the dual-Purkinje-image eye-tracker as explained above, we measured the onset time of the second saccade, which reached the correct target, and called these well-defined times a step-saccade choice response time (SCRT). The duration of the small second saccade would only add a small time to SCRT, and, being constant across NA conditions, would not affect our analysis of the NA effect on response time. We also measured the first-saccade latency (FSL), i.e., the onset time of the first saccade in these two-saccade responses. Note that the first saccade in this example was correctly aimed toward the target, but stopped short of it, whereas in other trials, it was incorrectly directed, as shown by an example in Fig. 1d. To be scored as a correct response a single-saccade or two-saccade response had to reach within a half-degree radius circle surrounding the correct target.

Results

The unexpected appearance of the two-saccade responses in our paradigm raised a difficult issue concerning what was the most logical event to measure in order to compare our results for saccades to those obtained by Hick (1952) and others in manual response tasks, as well as those by Kveraga et al. (2002) in which presumably only single-saccade responses were observed. This is a thorny issue because the fraction of correct saccades that were two-saccade responses increased as a function of NA, thus potentially confounding the analysis. Figure 1e shows the percent of two-saccade responses (both types of response shown in Fig. 1c and d included) for all correct saccades.

Two-saccade responses appeared in four out of the five subjects: no two-saccade responses were observed in S4. The fraction of such responses increased as a function of NA and reached a level around 50% in three subjects for the 8-NA condition.

Given this ambiguity regarding which movement to take for testing Hick's law in two-saccade responses, we took the most conservative approach in a first comparison and only used CRT data obtained when the response was a correct single-saccade (the type shown in Fig. 1b).

Single-saccade results

The distribution of CRT recorded from the five subjects is shown in Fig. 2a. The distributions shifted rightward by approximately the same amount as NA doubled. The percentile plot in Fig. 2b shows this logarithmic relationship more clearly where lines connect equal percentile CRT levels across NA by 10% increments from 10 to 90% with the median line marked red. A logarithmic relationship was consistently observed across all subjects (Fig. 2c, *bottom panel*). A linear regression between CRT and $\log_2$(NA) was highly significant for all subjects (p <0.0001,

Table 1). Although the slope of the regression for subject 5 was shallower than those for other subjects, it was still significantly different from zero (41.3 ms/bit with the 95% confidence interval of 21.0–61.6 ms/bit). The performance of all subjects in the task was close to perfect except in 8-NA trials (Fig. 2c, *top panel*). Given the data of CRT and performance combined, a speed-accuracy trade-off can be ruled out as an explanation for the CRT change. Therefore, we conclude that the choice response time for saccades increases as a logarithmic function of NA in agreement with Hick's law.

Following an approach introduced by Carpenter and his colleagues (Carpenter and Williams 1995; Reddi and Carpenter 2000; Reddi et al. 2003), we plotted the cumulative probability of CRT on a probit scale as a function of the reciprocal of CRT. This is done to take advantage of the fact that the reciprocal of response time obeys a Gaussian distribution and will form a straight line in such a plot. First, we tested whether this was in fact the case in our data using the Kolmogorov-Smirnov one-sample test. All sets of reciprocal-CRT distributions were compatible with a normal distribution (p >0.1, except 2-NA condition in S2 and 8-NA in S3 where p =0.08 and p =0.07, respectively).
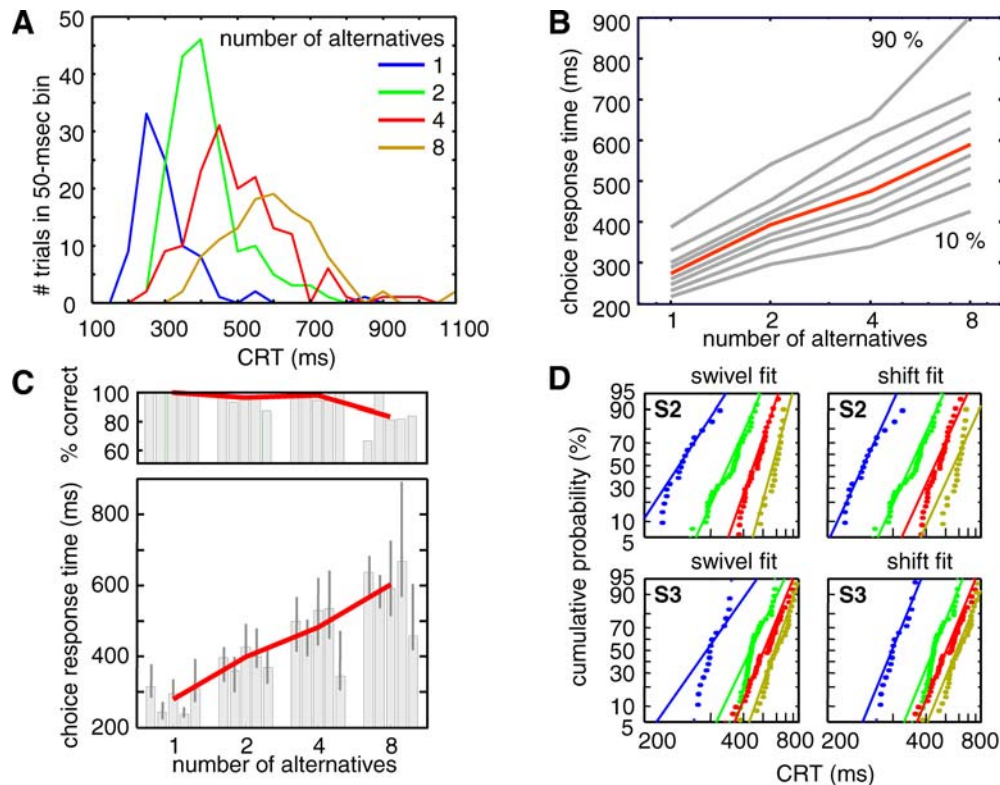

Fig. 2 a The distributions of CRT of single-saccade trials are plotted for different NA conditions. As indicated in the inset legend, the *blue curve* is for NA of 1 condition, the *green* for NA of 2, the *red* for NA of 4, and the *yellow* for NA of 8. **b** Averaged data from all five subjects showing the distribution of response times for each NA condition. Each gray curve represents the same percentile of CRTs across different NA conditions. The median, i.e., 50%, CRT curve is shown in *red*. **c** The percent correct (the *upper panel*) and median CRT (the *lower panel*) of individual subjects is shown by bars with the group data marked by *red curves*. *Vertical lines* over the bars indicate the 25–75% percentile range of CRT. **d** Reciprobit plots of RT distributions for two subjects (S2 and S3). The set of lines superimposed on the data in the *left panels* are by a swivel fit in which regression lines have a common x intercept, and that in the *right panels* by a shift fit where the slope of the lines is identical. The color of regression lines and data points indicates NA conditions as in **a**. See text for details concerning the analysis using reciprobit plots

Table 1 Results of a linear regression of CRT vs. $\log_2$ (NA) are summarized for each subject. The slope of a regression, i.e., b in the unit of millisecond per bit, is inversely related to an information rate (bit per second) which measures how fast information is transferred through a channel. A bit is a unit of information that equals to the amount of uncertainty reducible by a binary disambiguation. In the context of our study, it pertains to the number of doubling NAs. For example, NA of 8 is 3 bits higher in information than NA of 1

	Regression with CRT = a + b $\log_2$ (NA)		
	a (ms)	b (95% confidence interval) (ms/bit)	1,000/b (bit/s)
S1	331.6	87.5 (63.3–111.8)	11.4
S2	247.8	112.8 (94.1–131.5)	8.9
S3	332.4	107.2 (83.6–130.8)	9.3
S4	266.2	148.8 (125.8–171.7)	6.7
S5	340.2	41.3 (21.0–61.6)	24.2

A reciprobit plot of CRT data may reveal the characteristics of the underlying decision processes: a slope change (swivel) in the linear regression lines as NA increases in the reciprobit plots may be related to a change in the level of prior probability of a particular target appearing or the decision criterion for a decision process, while a parallel shift of the regression lines may reflect a change in the rate of rise from the baseline to the criterion (Reddi and Carpenter 2000; Reddi et al 2003). We therefore examined whether a swivel in regression fits or a shift in the set of regression lines fit our data better, in order to determine whether a criterion adjustment or a change in rate of rise of information transfer underlay the NA-dependent changes in CRT that we observed. A measure of goodness-of-fit was computed as the difference of log-likelihoods between two different maximum-likelihood (minimal χ^2) estimation procedures: one that best fit the data with a constraint that a set of regression lines should have a common intercept regardless of the slopes (a swivel fit), and the other with a constraint that the lines had an equal slope (a shift fit). Data from all but one subject favored a swivel fit over a shift fit (Table 2). Cases where a swivel fit was most favored (S2) and a shift fit was better than a swivel fit (S3) are shown in Fig. 2d. We conclude that the data favor a criterion adjustment as the reason for the observed NA-dependent changes in CRT.

Table 2 Using a χ^2-test, the goodness of fit is compared between a swivel (changing slopes with a constant intercept) fit and a shift (a constant slope) fit. In this test, the smaller the χ^2 and the larger the log-likelihood, the better is the fit. In our analysis, a positive value of log-likelihood difference means a swivel being favored over a shift fit, and a negative one vice versa

	Goodness-of-fit analysis			
	χ^2 in swivel fit	χ^2 in shift fit	d.f.	Log-likelihood difference
S1	10.23	16.3	52	9.23
S2	13.62	32.53	79	25.25
S3	26.04	16.58	94	−16.62
S4	24.46	28.15	91	4.61
S5	10.83	16.29	58	9.22

Including two-saccade responses in the analyses

As noted above, the eye movement responses in our paradigm often consisted of two-steps of small saccades as shown by the examples in Fig. 1c and d, even though the target was at a relatively small eccentricity of 5 deg. These step-saccades were more frequent with high NAs, reaching up to about 50% with 8 NAs in some subjects, while none was observed in one individual (Fig. 1e).

The first saccade of two-saccade responses was hypometric in amplitude, but often appeared rather accurate in direction, as illustrated in Fig. 3a. This plot of the direction error of the first saccade against its amplitude further revealed that the first saccade of these two-step responses fell into two categories. When the first saccade was larger than half a degree, the direction error was clustered around zero, indicating that the saccade was correctly directed toward the target, even though the amplitude was short. In contrast, in trials where the first saccade was less than half a degree in amplitude, the direction error was uniformly distributed with no sign of predilection toward a target.

This divergence of the first saccades into two categories was bolstered by another feature of the two-saccade responses, namely the inter-saccadic interval (ISI) between the first and subsequent corrective saccades reaching the target. The ISI was measured from the beginning of one saccade to onset of the second. The distribution of ISI in trials with the first saccade less than half a degree in amplitude was widespread (Fig. 3b, *top*), while the distribution was tightly clustered and peaked at about 120–130 ms in trials with the larger first saccades (Fig. 3b, *bottom*). This shows a tight temporal linkage between the first saccade and the subsequent saccade in the latter cases, contrasted with a weak relationship between saccades in the former cases.

The latency of the first saccade in the two-saccade responses was not correlated with its amplitude (Fig. 3c). The regression between the latency and amplitude was not significant for first saccades that were greater than 0.5 deg (R^2=0.019, p >0.14). (It reached a significant level when smaller first saccades were included in the analysis (R^2=0.030, p =0.0187), again suggesting that the two groups of first saccades were different from each other.) Nor did the latency change with NA: the latency of first saccades, i.e., FSL, was not different across NA conditions (p >0.1, Kruskal-Wallis non-parametric one-way ANOVA).

Given these results, we wondered whether our conclusion above that saccades obey Hick's law would still be valid when the two-saccade trials were included in the analysis. The analysis was performed twice, once by regarding the first saccade of a trial as a choice response (i.e., FSL in two-saccade trials), and the other by regarding a saccade that reached the target as a choice response (i.e., SCRT in two-saccade trials). Note that in single-saccade trials the first saccade reached the target, and therefore CRT of such trials was equivalent to both FSL and SCRT at the same time. Since the number of two-saccade trials was too few for NA of 1 and 2 to yield a reasonable
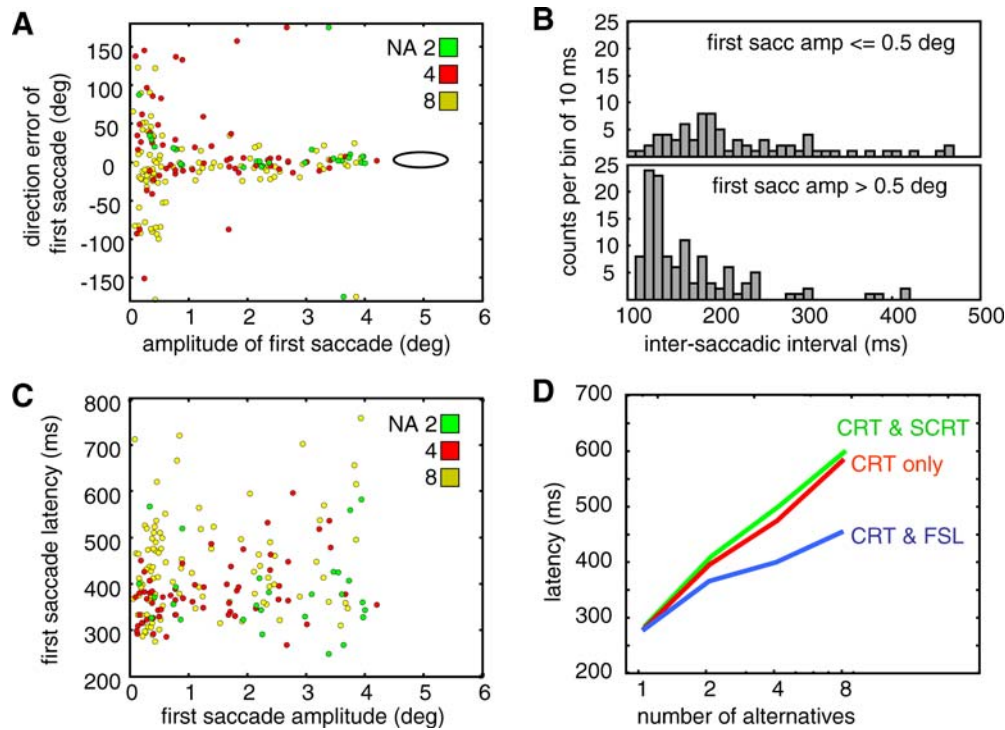
Fig. 3a–d Properties of saccades in two-saccade responses. **a** Direction error of the first saccade in two-saccade response trials is plotted as a function of the amplitude of the first saccade. The direction error was computed with respect to the target location in each trial. *Color* of the data points indicates NA condition: *green* for NA of 2, *red* NA of 4, and *yellow* NA of 8. The ellipsoid centered at 5-deg amplitude and zero-direction error schematically depicts a window reached by a later saccade so that the trial was counted as correct. **b** Distributions of the interval between the first and second saccades are shown for trials where the first was less than or equal to 0.5 deg in amplitude (*top panel*) and for those where it was greater (*bottom panel*). **c** The latency of the first saccade in two-saccade responses is plotted against its amplitude. Color coding of data points is the same as in **a**. **d** Median choice times pooled for all subjects and analyzed for all trials including two-saccade trials are plotted for different NA conditions. The *blue line* is the result obtained by taking the onset of the first saccade in a trial as a choice response time (i.e., by pooling CRT of single-saccade trials and FSL of two-saccade trials). The *green line* shows the results when the onset of a saccade reaching a target was regarded as a choice response (i.e., pooling the same CRT in single-saccade trials and SCRT in two-saccade trials). For comparison, CRT of single-saccade trials (only are shown by the *red line* identical to that shown in Fig. 2b)

statistic, we pooled the data from two-saccade trials with CRT of single-saccade trials for these analyses. As shown in Fig. 3d, while taking the first saccade of any trial as a choice response (i.e., FSL and CRT pooled together) made the curve deviate from linearity in this log-linear plot (the blue curve), choosing SCRT as a choice response in two-saccade responses and pooling them with CRT of single-saccade trials (the green curve) hardly changed the logarithmic relationship obeying Hick's law shown with single-saccade trials only (the red curve, the same as in Fig. 2b). It appeared then that, even though the eyes could make a rapid first saccade directed toward the target in some trials when faced with a difficult choice decision, the total time taken to reach the target ended up being about the same on average, regardless of the number of steps by which the target was reached.

Discussion

Two major findings from this study are the following: first, saccadic choice response time increases in the same way as that reported for other response types, when the number of alternatives in choice decision increases, provided that a stimulus-response translation is required. Second, when choice decision takes a longer time with more alternatives, saccades are often triggered with correct specification of the direction, but not of the amplitude. We will first discuss the implications of our results within the context of psychological models of choice reaction time, and then provide accounts of the possible mechanisms underlying the production of the two-saccade responses in which amplitude and direction seem to be dissociated.

Response time in choice decision

The slope of CRT-$\log_2$ (NA) plot in our data was found to be 110.3 ms/bit, i.e., the information rate of 9.1 bit/s (Fig. 2b, the *red line* plotting the median CRT of single-saccade trials), which is slightly higher than the 5–7 bit/s reported in studies using manual responses (Hick 1952; Hyman 1953) and lower than the 14–17 bit/s found in studies using verbal responses (Morin et al. 1965; Oldfield and Wingfield 1965). We therefore conclude that the saccade system is quite comparable with other response

systems in obeying Hick's law. The law pertains to choice decision making when multiple alternates exist, a cognitive process that more than likely operates the same across different response modalities.

Hick originally found that $CRT = b * \log_2 (NA+1)$ fit his results better than $CRT = b * \log_2 (NA)$, and suggested that the 1 was required because there was an additional possibility that no signal appeared. Welford (1960, p 62) later pointed out that the temporal uncertainty as to whether or not a target would be present, and if so when, may not always be equivalent to the one alternative, and proposed to call the latter formulation Hick's law. In this formulation, NA is to be understood as the equivalent total number of equally probable alternatives, and a constant may be added for time lags in the making or recording of a response. We took the latter equation for the analysis of our data, since the temporal uncertainty factor in our experiment was rather small: no catch trials were given in which no cue appeared, and, although we varied the fixation period preceding the cue onset between 600 and 1,200 ms, subjects reported that they could anticipate the cue onset roughly. This short interval is to be compared to Hick's experiment where the inter-trial interval was about 5 s, which was presumed to be quite beyond human span of time-tracking, maximizing the temporal uncertainty of a signal onset.

We found that our data could be better described by a slope change in the linear regression fits as NA increased rather than a parallel shift in the regression fits in a majority of the subjects. This indicated to us that the change in a decision process underlying the logarithmic change in CRT is more likely related to a change in the baseline signal reflecting prior probability, or a change in a decision criterion (Reddi and Carpenter 2000; Reddi et al. 2003) rather than a change in the rate of information transmission. It is quite plausible that the baseline activity of a neural population where the choice decision is made is modulated in a similar manner as described for buildup neurons of the superior colliculus (SC). Basso and Wurtz (1998) observed a consistent reduction in the activity of the cells as the probability of a target for saccades decreased. It is equally plausible that the slope change across NA conditions is produced by subjects' changing their criteria for reaching a decision, as proposed by the criterion-adjustment model for Hick's law (Usher et al. 2002).

Possible mechanisms responsible for two-saccade responses

The finding that some choice responses, particularly in the larger NA conditions in our paradigm, consisted of two-saccade responses was unexpected. The smaller (<1/2°) first saccades that was found to be incorrect in both direction and amplitude were most likely microsaccades, a type of fixational eye movement (Martinez-Conde et al. 2004, for a recent review). Their frequent occurrence in high NA conditions is probably secondary to the lengthening of movement latencies (Fig. 1) with longer-duration target choice decisions.

The larger (>1/2°) first saccades, on the other hand, seem a part of the choice response that directed the eyes toward the selected target. Truncated saccades that are followed at short latency have been reported before (Becker and Juergens 1979; McPeek et al. 2000), but the two-saccade responses we recorded here are different in that the first movement was correctly directed, but too short in amplitude. Step-saccades in the same direction that together place the eyes on target have previously been observed in normal subjects as well as Parkinson's disease (PD) patients, especially in memory-guided saccades (Kimmig et al. 2002) and in antisaccade tasks (Hallett and Adams 1980).

The fundamental question that must be answered is why saccade direction is correct, but amplitude short in the two-saccade responses. In most present models of saccade generation, the initiation, maintenance and the direction of saccades results from the interplay of three signals: a trigger signal, a maintenance signal and a metric drive signal (Scudder et al. 2002). The first two signals are inhibitory and project to the omnipause neurons (OPNs) in the brain stem. The drive signal is excitatory and goes to burst neurons also in the brain stem. In the model of saccade generation of Findlay and Walker (1999), the first signal is referred to as the "when" signal and the third signal as the "where" signal. In reflexive saccade paradigms the when and where signals develop rapidly and synchronously over time so that a fully developed where signal is present when the trigger signal turns off the OPNs and starts the saccade. The nature of the maintenance signal is less well known, but it is likely to develop more slowly than the trigger signal, and is maintained in time as the saccade progresses, whereas the trigger signal is very brief in time. There is experimental evidence for the existence of, and this temporal shape of, these two signals from intracellular recordings in cat OPNs during saccades (Yoshida et al. 1999). An additional assumption incorporated in most saccadic system models is that OPNs have a sharp threshold level for inhibitory input so that they turn off quickly when the trigger signal drives their cell membranes below the threshold level, but they also turn back on rapidly when the combined inhibition from the trigger and maintenance signals rises back above this level (Van Gisbergen et al. 1981).

In order to explain our two-saccade results we hypothesize that the drive signal is related to the population activity on the SC motor map and that the maintenance signal is temporally related to the SC drive signal, but is converted to an inhibitory signal at the level of the OPNs. During visually guided saccades, activity at the desired target location in the SC (and hence, both the drive and maintenance signals) builds up and peaks just before saccade onset and then declines as the movement progresses (Anderson et al. 1998). The trigger signal is generated in synchrony with the peak of the SC activity.

However, recordings in monkey during more cognitively controlled saccades like memory-guided saccades

have shown that activity in the caudal SC is weaker than that recorded for visually guided saccades (Stanford and Sparks 1994; Munoz and Wurtz 1995). We hypothesize that saccades made as a choice response have similar patterns of activity in the SC. Activity in the SC in our high NA conditions is liable to be even weaker and delayed than in memory-guided movements because more color-to-location associations require more time to process. This situation could lead to a temporal dissociation between the inhibitory trigger signal and the maintenance signal to the OPNs. The chromatic change in the fixation spot (cue) may have been sufficient for specifying when to make a saccade response (generation of the trigger), but signals for maintenance of the saccade would required more time to develop through further processing of the new color information. Nevertheless, the build up of activity in the SC, although weaker than that for visually guided saccades, would still be centered at the desired target location. This weaker activity would specify the correct direction of the first saccade, but would not be sufficient to sustain it. As the activity in the SC continued to build up after the truncation of the first saccade, a new threshold would be reached and a second movement would be triggered.

The mechanisms that we propose for the two-saccade responses in the choice response paradigm have some similarity with the interrupted saccades produced by omnipause neuron (OPN) or rostral SC stimulation (Keller and Edelman 1994; Keller et al. 1996; Munoz et al. 1996) and with the mechanism proposed to explain the fractured saccades observed in late-onset Tay-Sachs disease (Rucker et al. 2004). In these cases saccades are triggered in a normal fashion, but then are assumed to be truncated by the premature return of discharge in the OPNs.

Alternately, if the information from the presentation of the color cue at the fixation point interferes in some way with the normal cerebellar mechanisms that terminate saccades (Fuchs et al. 1993), then the cerebellar output to the saccadic burst generator may be the cause of the short amplitude first saccades (Quaia et al. 1999). The same region of the fastigial nuclei that is posited to control the end of saccades also projects to the rostral colliculus (May et al. 1990). This region of the fastigial nucleus also projects to the omnipause neurons and the burst cells that receive the SC drive signal (Noda et al. 1990). Thus, a cerebellar mechanism may be involved in the generation of two-saccade responses.

In any case the short inter-saccadic interval (Fig. 3b, *lower panel*) between the first and second saccades in correctly directed two saccade-responses supports the hypothesis that these are in fact a single saccade that is interrupted by threshold mechanisms at the level of the OPNs.

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