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## Saccades operate in violation of Hick's law

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**Abstract** Hick's law states that response times (RTs) increase in proportion to the logarithm of the number of potential stimulus-response (S-R) alternatives. We hypothesized that time-consuming processes associated with response selection contribute significantly to this effect. We also hypothesized that the latency of saccades might not conform to Hick's law since visually guided saccades can be automatically selected using topographically organized pathways that convert spatially coded visual activity into spatially coded motor commands. We evaluated these hypotheses by examining three response modalities for their compliance with Hick's law: saccades directed to a visual target (prosaccades), saccades directed away from the target (antisaccades) and manual responses in which each digit was associated with a specific target location (key-press responses). Both antisaccades and key-press responses conformed to Hick's law but saccade latencies were completely unaffected by S-R uncertainty. The significance of these findings is considered in terms of the processes of response selection and premotor programming.

**Keywords** Eye movements · Saccades · Antisaccades · Stimulus-response uncertainty · Manual responses

### Introduction

The ability to rapidly select the most appropriate response from a larger set of potential alternative responses is an essential feature of adaptive behavior. In the species that rely on saccadic eye movements to sample their visual surroundings, we might expect that selection pressures have perfected the neural mechanisms that convert specific sensory inputs to specific saccadic eye move-

ments. Indeed, the anatomical arrangement of the superior colliculus (SC) is well suited to produce saccades that align the fovea with eccentric stimuli. Saccadic eye movements are coded in the SC by a locus of activity within a population of premotor neurons (e.g., Schiller and Koerner 1971; Wurtz and Goldberg 1971, 1972; Robinson 1972; Schiller and Stryker 1972; Sparks 1975; Mays and Sparks 1980). A topographic projection of visual afferents within the SC creates a retinotopic map that lies in spatial register with this "motor map" of saccadic directions and amplitudes (cf. Sparks and Hartwich-Young 1989). Although saccadic adaptation is a well established phenomenon, there does not appear to be any compelling reason to incorporate a great deal of plasticity in the connections between visual inputs and saccadic directions.

On the other hand, a unique natural coupling between sensory inputs and motor outputs may not exist in systems that mediate other types of sensorimotor coordination. Consider, for instance, the control of the fingers. Even though humans are readily capable of precise visual control over manual movements, it is not clear that specific sensory inputs should be associated with specific finger movements. Indeed, when it comes to visual guidance of the hands and fingers, flexibility in the sensorimotor connections may be most advantageous. However, flexible mappings of sensory inputs onto motor outputs may have a cost, as variations in stimulus-to-response (S-R) mapping have a large influence on how quickly and efficiently the appropriate response can be effected (e.g., Fitts and Seeger 1953; Griew 1964; Alluisi et al. 1964; Alluisi 1965; Broadbent and Gregory 1965; Spigel 1965). An increase in response latency is one of the costs we may expect to pay for flexibility in sensorimotor coordination.

Hick's law refers to the commonly found relationship between response latency and S-R uncertainty, and states that as the number of S-R alternatives increases, so does response latency (Hick 1952). Specifically, response latencies vary as a log function of the number of S-R alternatives:

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$$RT_m = c + d \cdot \log n, \quad (1)$$

where  $RT_m$  is the mean reaction time,  $c$  and  $d$  are parameter values, and  $n$  is the set of potential S-R alternatives. Hick's seminal experiments examined manual key-press tasks in which each key was associated with a different visual target. A great deal of subsequent work has established the validity and generality of Hick's law (e.g., Hyman 1953; Alluisi et al. 1964; Alluisi 1965; Broadbent and Gregory 1965; Spigel 1965; Mahurin and Pirozzolo 1993; Vickrey and Neuringer 2000).

The generality of this relationship between S-R uncertainty and reaction time led to its designation as a "law," but a few tasks that apparently do not comply with it have been reported, such as oral and pointing responses to lights (Brainard et al. 1962; Morin and Forrin 1962, 1965; Fitts 1964). One characteristic that oral responses may share with saccades is that they are both highly overlearned tasks in normal subjects.

Whether saccades conform to Hick's law is uncertain. Of the studies that measured saccadic latency while varying saccade target direction, most have reported increases in saccadic RT when one or more saccadic target parameters are uncertain (e.g., Hackman 1940; White et al. 1962; Megaw and Armstrong 1973; Heywood and Churcher 1980; Abrams and Jonides 1988; Dorris and Munoz 1998, Cameron 1995), while some have found no such increase (Saslow 1967b).

We hypothesized that S-R uncertainty may not have an effect on the latency of saccadic eye movements because of the highly efficient mapping in the primate SC used to translate stimulus locations into the appropriate oculomotor commands. Since antisaccades (voluntary saccades that are directed away from the target) cannot take advantage of this sensorimotor arrangement, we further hypothesized that antisaccades should conform to Hick's law. We tested these hypotheses by comparing prosaccadic, antisaccadic, and manual key-press response latencies under different levels of S-R uncertainty.

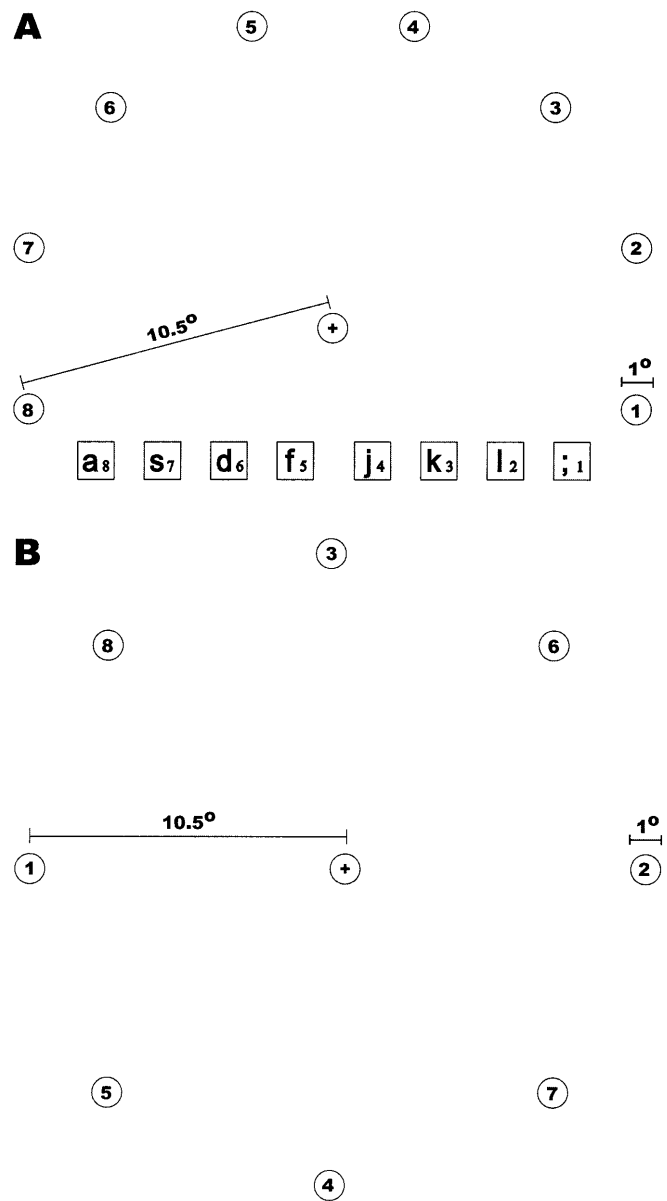
## Materials and methods

### Subjects

A total of six subjects participated in the study; a subset of three subjects participated in all three experiments. All subjects were healthy Dartmouth College students or staff and had normal or corrected-to-normal vision. Except for two of the authors, all subjects were naïve with respect to the purpose of the study. Each subject was informed about the nature of the recording procedures, the general goals of the experiment, and signed an informed consent document. The Dartmouth College Committee for the Protection of Human Subjects approved the experimental protocol followed in this report.

### Stimuli

Stimuli were presented on a computer-controlled video monitor at a viewing distance of 57 cm. Targets were disks  $1^\circ$  in diameter whose luminance was  $27.4 \text{ cd/m}^2$ . Target outlines were circles one pixel in thickness whose average luminance (encompassing both the circle

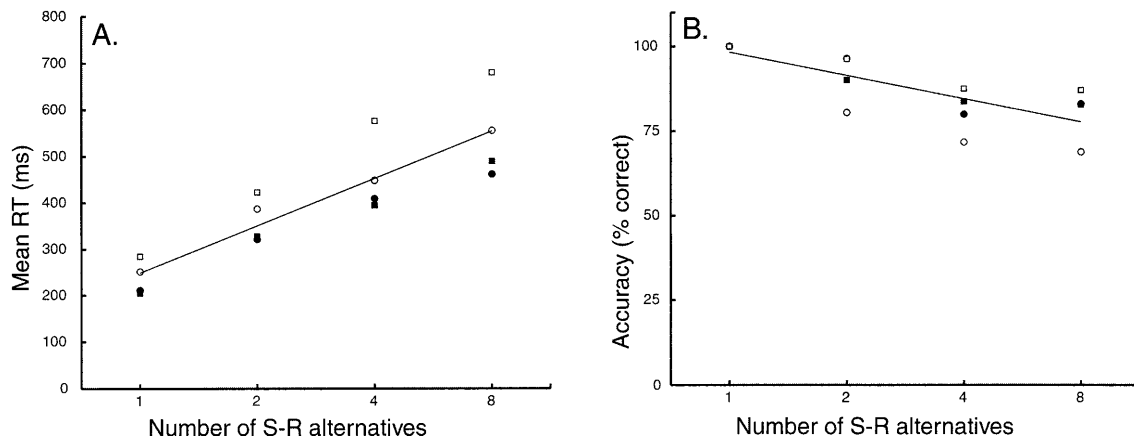


**Fig. 1A, B** Stimulus display. **A** The semicircular arrangement. The *subscripts on the keys* indicate which target the key was associated with. **B** The circular arrangement

and the dark pixels within it) was approximately 1/7th that of the targets. The background luminance was  $<1 \text{ cd/m}^2$ . Targets were arranged into two different spatial configurations: a semicircular arrangement similar to that used by Hick (1952) and a circular arrangement (Fig. 1A, B, respectively). The semicircular arrangement was used for the manual key-press and the prosaccade tasks, while the circular arrangement was used for the pro- and antisaccade tasks. All stimuli were drawn with a single screen refresh. Their duration was managed by a low-level subroutine that controlled the refresh rate of the display and yoked the timing of all critical intervals to it.

### Procedure

Trials were blocked depending on target set size; there were either one, two, four, or eight possible target locations. We refer to this



**Fig. 2A, B** The effects of S-R uncertainty on manual key-press responses. The *symbols* represent **A** manual latency means and **B** accuracy rates for each observer

variable as *level of S-R uncertainty*. Throughout the block, target outlines indicating the possible target locations remained illuminated to make the number of possible response alternatives salient to the subject. The start of each trial was indicated by the onset of the fixation disk. Following a fixation period ranging from 600 to 1,600 ms, the fixation disk was removed except for its outline, and a peripheral target simultaneously filled one of the possible target outlines. The target remained for 1,000 ms and was then extinguished, leaving only the outline once again. The next trial was indicated by filling in the fixation disk's outline.

In all experiments, the instructions to the subjects emphasized both speed and accuracy. In the *manual key-press* experiment, subjects had to press the key associated with the location that contained the target. In the *prosaccade* experiment, subjects were instructed to look at the target as soon as it appeared and to return their gaze to the fixation dot once the target was extinguished. In the *antisaccade* experiment, subjects were asked to look at the target outline 180° opposite to the target and to return to the fixation dot once the target was extinguished. Note that in our antisaccade task, subjects actually made a saccade to a marked location (i.e., the target outline), but the cue to look at the marked location was located 180° away from that location.

Within a block, the level of S-R uncertainty remained constant. In each block, the location of the target was randomized, with each location being used a total of 16 times per block. Thus, a block with a target set size of 1 had 16 trials, a block with a target set size of 2 had 32 trials, and a block with a target set size of 4 had 64 trials. For the 8 target condition, we divided the block size (128) in half for subject comfort reasons; therefore, there were two blocks of 64 trials each in the 8 target condition. The order of blocks was randomized across subjects. In the one target condition, there were actually two target outlines present (the cueing location and the antisaccade target location), but the cueing location remained constant within a block of trials. Therefore, the subject always had to make an antisaccade to the same location in this condition.

In all three experiments, subjects completed a minimum of 32 trials per target for each level of uncertainty, with the mean correct number of trials *per condition per target* ranging from 32 to 62 in all experiments.

#### Apparatus

##### *Acquisition of eye data*

Horizontal and vertical eye position was monitored using the scleral search coil technique (Robinson 1963) worn on the right eye of subjects who were seated in the center of a 2-m magnetic field coil

(Remmel Labs.). We monitored head position using a second coil placed on the forehead. The latter recordings confirmed that the subjects kept their heads stationary, and were not analyzed further. The resolution of the recording system is 10 min of arc. Eye and head position was digitized (16-bit resolution, 200 Hz) and stored on disk. A calibration procedure required fixation of lights positioned in the center and the corners of the 19" CRT display used for the experiment. Calibration data were obtained at the beginning of each experimental session. These data were used to transform the raw voltage records to measures of angular displacement. Saccades were detected automatically using a velocity criterion (37.5°/s). As suggested by the manufacturer of the search coils (Skalar Medical), experimental sessions were confined to 30 min and subjects were tested on alternate days.

##### *Acquisition of manual key-press data*

The key-press responses were collected with a conventional computer keyboard. A spatially compatible mapping of the target locations onto the individual keys was adopted which was similar to that used by Hick (1952). As indicated in Fig. 1A, the keys were associated with target location based on their approximate horizontal alignment with the "home row" keys, i.e., the rightmost target was associated with the rightmost key [";"], which was depressed using the little finger of the right hand. Subjects had to respond with 90% accuracy in a practice session before proceeding to the formal collection of data. All subjects were able to achieve the criterion of 90% accuracy during this practice session.

##### *Computers and data analysis*

The timing and sequence of the stimuli were controlled by an IBM PC running DOS. The stimulus control program yoked target onsets and offsets with the vertical refresh rate of the CRT display. The stimulus control program signaled target presentation and synchronized the operation of a data acquisition computer with signals sent via the PC's parallel port. A Macintosh computer running a data acquisition program written in LabVIEW (National Instruments) digitized the control and target onset pulses, the search coil, and in the key-press task, the output of a computer keyboard. The data acquisition program stored the position of subjects' head and right eye, the target location, onset time, and for the manual responses, the relevant key-press information. All data analysis was performed offline. Statistical analyses were performed using the statistical package SPSS 9.0 for Windows (SPSS, Inc., 1989–1999) and Matlab 5.3 for Windows (The MathWorks, Inc. 1984–1999).

**Table 1** Response latencies as a function of S-R uncertainty.  $N$  is the mean number of trials collected per subject for each target at that level of S-R uncertainty

Number of S-R alternatives	1	2	4	8	
Response modality	Mean (SD, $N/t$ )	Mean (SD)	Mean (SD)	Mean (SD)	Best-fit line
Manual latency	238 (32.2)	364 (42.1)	456 (71.6)	546 (84.1)	$y=146.99+101.63x$
Prosaccades	206 (17.1)	206 (5.8)	202 (5.5)	203 (3.9)	$y=206.01-0.35x$
Antisaccades	210 (5.9)	259 (14.9)	299 (12.4)	320 (5.3)	$y=179.98+36.89x$

**Table 2** Accuracy as a function of S-R uncertainty

Number of S-R alternatives	1	2	4	8
Response modality	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
Manual key-press accuracy (%)	100.0 (0)	90.8 (6.50)	80.8 (5.85)	80.5 (6.91)
Prosaccade accuracy (degrees)	1.74 (0.46)	1.36 (0.30)	1.64 (0.40)	1.66 (0.34)
Antisaccade accuracy (degrees)	1.76 (0.30)	1.65 (0.38)	1.93 (0.30)	2.21 (0.40)
Antisaccade direction accuracy (%)	99.99 (0.009)	93.1 (0.01)	86.3 (0.09)	75.2 (0.09)

## Results

### Manual key-press experiment

The purpose of this experiment was to verify that the present paradigm and procedures produce data consistent with Hick's law using tasks in which it is expected to apply. The results for correct responses are displayed in Fig. 2 and reported in Tables 1 and 2. All subjects exhibited an expected increase in reaction times (RTs) with increasing S-R uncertainty<sup>1</sup> (Fig. 2A). A planned comparison predicting a linear increase in the latency means as a function of  $\log_2$  of S-R uncertainty was also significant ( $F_{(1,14)}=47.0$ ,  $P<0.00001$ ), and accounted for 77% of the variance in the data. The accuracy of the responses (Fig. 2B) generally decreased as the latency means increased ( $F_{(1,14)}=22.8$ ,  $P<0.0004$ ), suggesting that the RTs were not contaminated by a speed-accuracy tradeoff. These results are entirely consistent with those obtained by Hick (1952), as well as many others (e.g., Hyman 1953; Broadbent and Gregory 1965; Mahurin and Pirozzolo 1993).

### Prosaccade experiment

The purpose of this experiment was to test our hypothesis that the latency of visually guided saccades will not depend on S-R uncertainty. The results are displayed in Fig. 3 and reported in Tables 1 and 2. As Fig. 3B illustrates, S-R uncertainty did not influence the latencies of prosaccades ( $F_{(3,12)}=0.17$ ,  $P>0.91$ ). This was confirmed by a non-significant planned comparison predicting a linear increase in latency means with  $\log_2$  of S-R uncertainty ( $F_{(1,14)}=0.03$ ,  $P>0.86$ ). The contrast accounted for only 0.2% of the variance. The accuracy of saccades was computed on the basis of the unsigned Euclidean distance from the center of the targets. As Fig. 3C

illustrates, the average accuracy did not vary with S-R uncertainty ( $F_{(3,12)}=0.79$ ,  $P>0.52$ ). We also examined the data for saccade *direction errors*, defined as a deviation of the saccade vector direction of more than  $\pm 22.5^\circ$  from the straight-line path from fixation to target. There were no instances of direction errors in the prosaccade task. Taken together, these results support our hypothesis that prosaccades do not conform to Hick's law.

### Antisaccade experiment

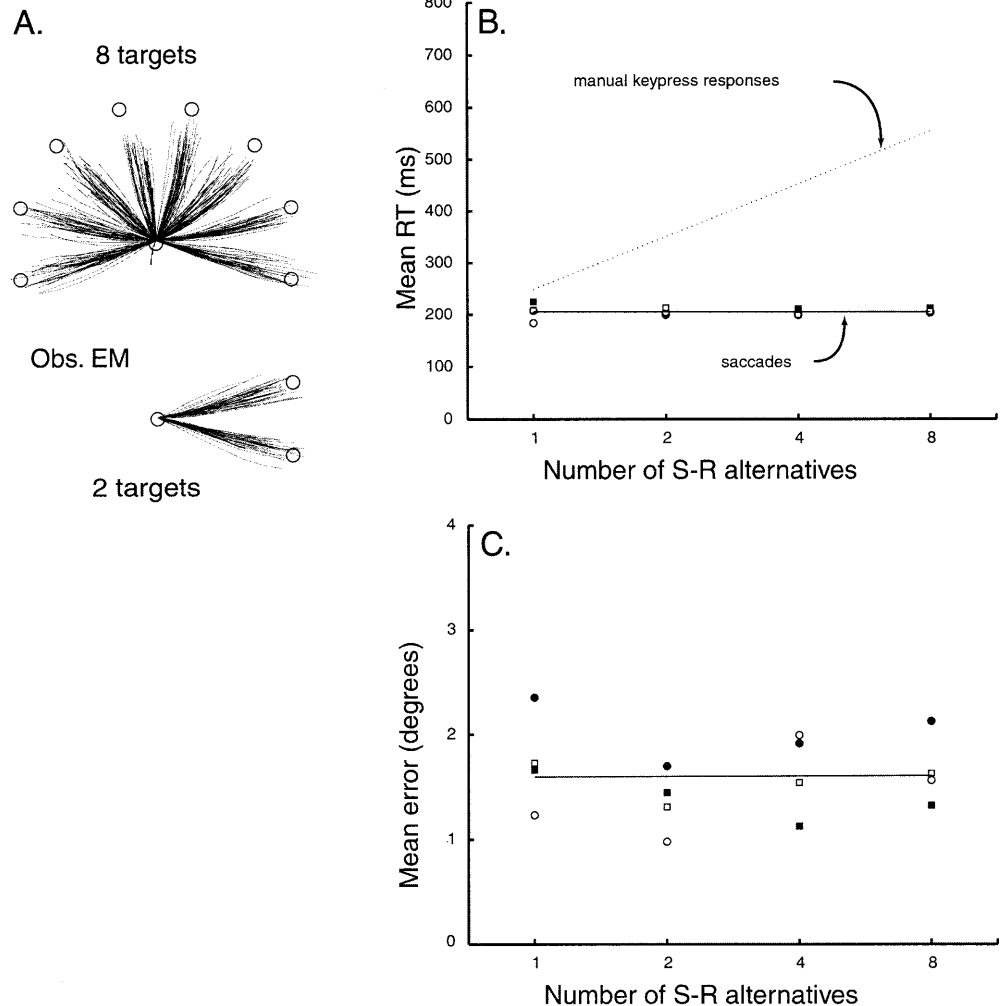
To determine whether saccadic eye movements will conform to Hick's law if they do not have the advantage of the natural mapping between visual and saccadic directions, we next examined the effects of S-R uncertainty on the latency of antisaccades. We modified the display from the semicircular to a circular arrangement of potential target locations. Subjects were required to redirect their gaze  $180^\circ$  from the location of the visual target ("look away" from the target). The experimental procedures were in all other respects identical to those used in the prosaccade experiment.

The antisaccade results are illustrated in Fig. 4 and reported in Tables 1 and 2. As Fig. 4B illustrates, mean RT for all subjects increased in proportion to S-R uncertainty. A planned comparison predicting a linear increase of the means was also significant ( $F_{(1,14)}=148.93$ ,  $P<0.00001$ ), and accounted for 92% of the variance. Endpoint accuracy did not strongly depend upon S-R uncertainty ( $F_{(1,14)}=3.60$ ,  $P<0.08$ ) (see Fig. 4C), suggesting that the latency data are not contaminated by a speed-accuracy tradeoff. Direction errors increased as a function of S-R uncertainty (linear contrast  $F_{1,14}=24.69$ ,  $P<0.0002$ ) (see Fig. 4D).

To control for the change in stimulus configuration, we had a naïve subject make prosaccades using the same (circular) stimulus configuration as that used for antisaccades. The RT means (218, 216, 217 and 210 ms for one, two, four and eight targets, respectively) did not show any increase as a function of S-R uncertainty and are

<sup>1</sup> Since we used  $\log_2$  of S-R alternatives as the independent variable, the data are analyzed with linear contrasts. For the same reason, the means are plotted on a log scale.

**Fig. 3A–C** The effects of S-R uncertainty on prosaccades. **A** Eye movement plots for observer EM in the eight target (*top panel*) and two target (*bottom panel*) conditions; **B** latency means; **C** error (unsigned Euclidean distance from the center of the targets) means for each observer



comparable to the same subject's means in the semicircular stimulus configuration (209, 213, 199 and 206 ms).

The observation that antisaccade latencies conform to Hick's law while prosaccades do not demonstrates that there is nothing about saccadic responses per se that protects them from the effects of S-R uncertainty. Rather, the two experiments together indicate that only natural saccades – those that take advantage of the spatial alignment of visual inputs with saccadic motor maps within the superior colliculus – appear immune to the effects of S-R uncertainty.

## Discussion

Our findings demonstrate that prosaccades are selected and programmed with equal facility irrespective of the level of S-R uncertainty. Thus, the prosaccade results violate Hick's law in that response latency does not increase with increasing levels of uncertainty. In contrast, both manual key-press and antisaccade latencies conform to Hick's law, as the response latencies in these tasks

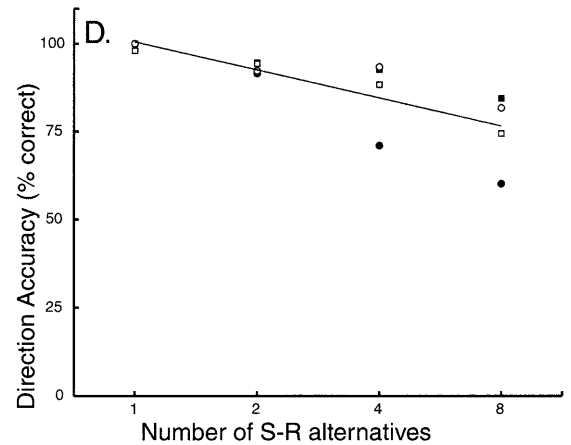
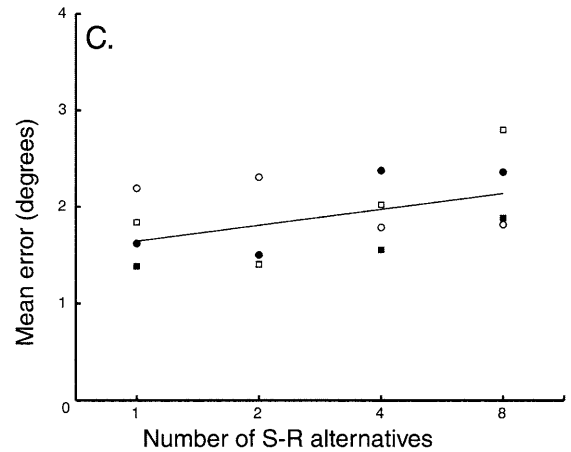
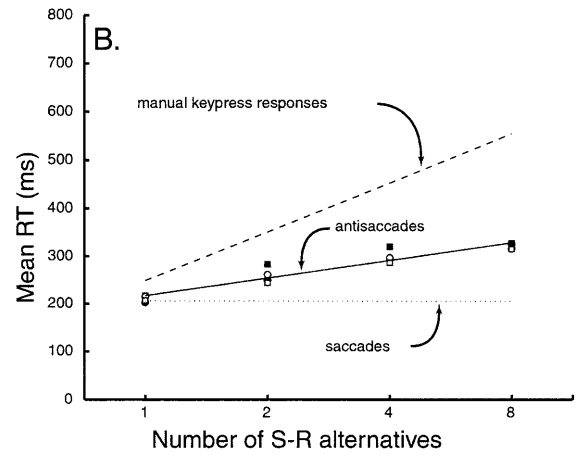
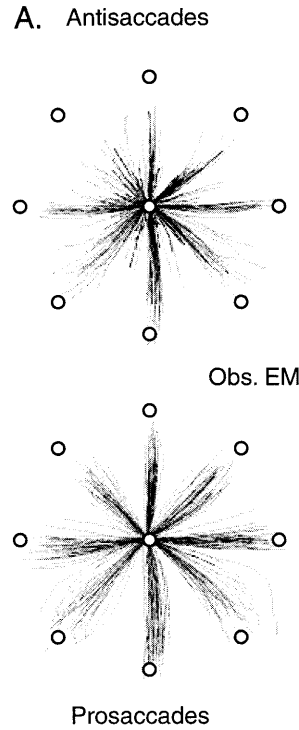
increased as a log function of the number of S-R alternatives.

### Response uncertainty and motor programs

Stimulus-response uncertainty could in principle influence the duration of any individual stage of processing that is involved in the performance of these tasks. However, the fact that prosaccade latencies were unaffected by S-R uncertainty implies that S-R uncertainty does not influence the time it takes for the visual system to identify the target – unless we assume that additional visual processing of the target is needed to select manual responses and anti-saccades. Thus, it is likely that these increases in RT occur after stimulus identification. This is consistent with other findings (e.g., Abrams and Jonides 1988) and suggests that in the tasks in which Hick's law is obeyed, the delays are incurred in the response selection stage (which may or may not include motor programming).

The finding that prosaccades are able to avoid the time costs associated with response selection raises questions

**Fig. 4A–D** The effects of S-R uncertainty on antisaccades. **A** Antisaccade eye movement plots for observer EM in the eight target (*top panel*) and *prosaccade* eye movement plots in the control, eight target (*bottom panel*) conditions; **B** antisaccade latency means; **C** error (unsigned Euclidean distance from the center of the targets) means; **D** accuracy rates for each observer



concerning the premotor programming of saccades. Phenomenologically, it seems self-evident that one can “create the intention” to redirect the gaze to a new location without actually doing so. This “feeling” of being prepared to make a saccade without actually moving one’s eyes is closely related to what many think of when invoking the idea of a motor program for a saccade. Both humans and macaque monkeys can make saccades to remembered locations, and the neural activity during the

saccadic retention intervals has often been interpreted as reflecting the maintenance of a “saccadic program,” or intention to make a saccade to that location (e.g., Basso and Wurtz 1997, 1998; Dorris and Munoz 1998).

The notion of a prepared response provides a plausible explanation as to why responses that are known in advance generally can be executed faster than those that are not. It also can explain why the latency of antisaccades is essentially equivalent to the latency of prosac-

cedes only when there is just one possible target – in both cases, the saccade metrics may be preset and the response then need only be triggered by the onset of a target (see Fig. 4). Yet, if we assume that response uncertainty necessitates a process of “response selection,” how can we explain the fact that prosaccades produced under conditions of response uncertainty are generated just as quickly as prosaccades to a location that is known in advance (see Fig. 3)? Since the latencies of prosaccades show no savings in RT when the response parameters are known in advance, we conclude that saccades made under response uncertainty must not require a time consuming process of response selection. We are left with the conclusion that while prosaccades can be preprogrammed, either our subjects did not preprogram them, or if they did, the preprogramming did not produce any savings in the time it takes to execute the response.

Are saccades special?

Saccades are not the only sensorimotor task that reportedly violates Hick’s law. Naming of visually presented numerals in one’s native language has generally been reported to be insensitive to response uncertainty (Brainard et al. 1962; Morin and Forrin 1962, 1965; but see Alluisi et al. 1964; Alluisi 1965 for contrary findings). It is worthwhile to consider what, if anything, the processes invoked by the two tasks might have in common. Further, a comparison of these systems may be very instructive if we wish to understand the mechanisms that enable fast and efficient mapping of stimuli and responses. One aspect that prosaccades and numeral naming have in common is that both tasks are overlearned responses. It is possible that when a sensorimotor task becomes overlearned, the strength and permanence of the S-R connections employed begins to approach in efficacy the “automatic” operation of the SC in producing visually guided saccades. Alternatively, it is also possible that in some response modalities such levels of performance can never be achieved, or that the necessary learning can only occur during critical periods in development. We are currently exploring some of these hypotheses.

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