An anti-Hick's effect in monkey and human saccade reaction times

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In order to execute movements to targets in the environment, we must first select a target in which to move, generally from an array of alternatives. Hick's Law states that reaction time (RT) increases as the number of response alternatives increases. Violations of this law, however, generally in the form of the *absence* of a relationship between response alternatives and RT have been reported in the literature. K. Kveraga, L. Boucher, and H. C. Hughes (2002), for example, found that saccades to visual targets violate Hick's Law. To examine this violation further, we measured saccade RTs in monkeys and humans and found that saccade RTs actually *decreased* as the number of potential target locations increased. We hypothesize that this arises because subjects must actively inhibit premature saccades, and that the required inhibition increases as the certainty of a movement to a particular location increases. With increased inhibition, saccade onset is delayed, resulting in an anti-Hick's effect.

Keywords: Hick's Law, eye movement, reaction time

Introduction

Hick's Law states that reaction time (RT) increases linearly with a $\log_2$ increase in stimulus–response (S–R) alternatives (Hick, 1952; Hyman, 1953). This "law," which is one of only a few in experimental psychology (e.g., Fitts'—Fitts, 1992; Weber–Fechner—Fechner, 1860/1966; Stevens'—Stevens, 1957), has been widely supported in the literature (e.g., Alluisi, 1965; Broadbent and Gregory, 1965; Hyman, 1953), under a variety of experimental conditions (for a review, see Teichner & Krebs, 1974), and has had far-reaching application from human factors research (e.g., Raskin, 2000) to theories of intelligence (e.g., Vickrey and Neuringer, 2000) to neural network models (e.g., Bogacz, 2007).

Violations of this law, however, generally in the form of the *absence* of a relationship between S–R alternatives and RT, have been reported in the literature (for examples, see Longstreth, el-Zahhar & Alcorn, 1985; Teichner & Krebs,

1974). Perhaps most noteworthy are saccadic eye movements to visual targets, which in some studies have been shown to obey Hick's Law (Abrams & Jonides, 1988; Hackman, 1940; Michard, Têtard, & Lévy-Schoen, 1974) while in other studies have been shown to violate Hick's Law (Heywood & Churcher, 1980; Kveraga, Boucher, & Hughes, 2002; Saslow, 1967), showing, for example, an increase in RT from 1 to 2 S–R alternatives but no increase in RT beyond 2 S–R alternatives (Kveraga et al., 2002).

While it is unclear as to why some studies have shown that saccades obey Hick's Law while other studies have shown that saccades violate Hick's Law, a number of factors have been shown to influence the relationship between S–R alternatives and RT. For example, studies have shown that practice decreases the intercept and the slope of the relationship between S–R alternatives and RT, indicating that not only do RTs decrease with practice, but also that the effect of S–R alternatives decreases with practice (Fitts and Posner, 1967; Heywood and Churcher, 1980; Longstreth et al., 1985; Teichner &

Krebs, 1974; Vickrey and Neuringer, 2000). In addition, studies have found that compatible responses, such as saccades executed to a cued target location (pro-saccades), violate Hick's Law, whereas incompatible responses, such as saccades executed in the direction opposite a cued target location (anti-saccades), obey Hick's Law (Kveraga et al., 2002; Abrams & Jonides, 1988; respectively). Thus, it is possible that because saccades to targets are a well practiced S–R compatible response, they do not show a Hick's effect, or if they do show a Hick's effect, it is much smaller than generally found in other response modalities.

In order to better understand the relationship between saccadic eye movements and S–R alternatives, and the factors that influence this relationship, we examined the effect of S–R alternatives in both monkeys and humans. Monkeys are particularly well suited for this research not only because they are capable of performing hundreds of trials across many sessions, but also because they provide a model system for studying the underlying neuronal substrate at the single cell level.

Experiment 1

The purpose of this experiment was to examine the relationship between saccade RTs and S–R alternatives in monkeys.

Method

Three adult male rhesus macaque monkeys (*Macaca mulatta*) and one adult male long-tailed macaque monkey (*Macaca fascicularis*) participated in the experiment. Monkeys were seated in a custom-designed monkey chair (Crist Instruments, Hagerstown, Maryland) in a sound-attenuated room. Stimuli were back-projected by a

CRT projector (Electrohome, Kitchener, Ontario) onto a screen located 25 cm in front of the monkey. Unlike an LCD projector, a CRT projector casts no extraneous light, so that other than the visual stimuli, experiments took place in complete darkness. Eye movements were monitored using scleral search coil techniques, digitized and stored at a rate of 500 Hz.

Monkeys performed a "center-out" saccade task (Figure 1). A trial began when the monkey fixated on a centrally located circle. The number of S–R alternatives was indicated by 1, 2, 4, or 8 white "placeholders" surrounding the centrally located circle. These circular placeholders (1 × 1 degree) were presented at 20 degrees of eccentricity and remained "on screen" throughout the session to signal the potential locations in which a target could appear. Following a variable delay of 350 to 1000 ms, one of the placeholders was filled in. This target appeared with equal probability in each of the placeholders (e.g., with 25% probability in each placeholder under the 4-placeholder condition, and with 100% probability in the sole placeholder under the 1-placeholder condition.) After the onset of the target, the monkey had 800 ms to saccade to within 5 degrees of the target location. The onset of a saccade was defined as the point at which eye velocity first exceeded 30°/s. A trial was aborted "online" if the monkey failed to achieve and maintain fixation until the target appeared, failed to move within 800 ms after the target appeared, or did not move to within 5 degrees of the target. Aborted trials were signaled to the animal by projecting a multi-colored pattern in the center of the screen. Completed trials were rewarded with a drop of fluid.

Monkeys failed to achieve initial fixation on 7.6% of trials. Late or inaccurate saccades occurred on only 3.3% of trials. For 1-, 2-, 4-, and 8-placeholder conditions, the error rates were 4.4%, 3.0%, 3.3%, and 2.5%, respectively. These trials, which were aborted online, were excluded from analysis. In addition, there were a percentage of trials which were not aborted online but were removed from analysis "offline." More specifically, we removed another ~6% of trials because the saccade
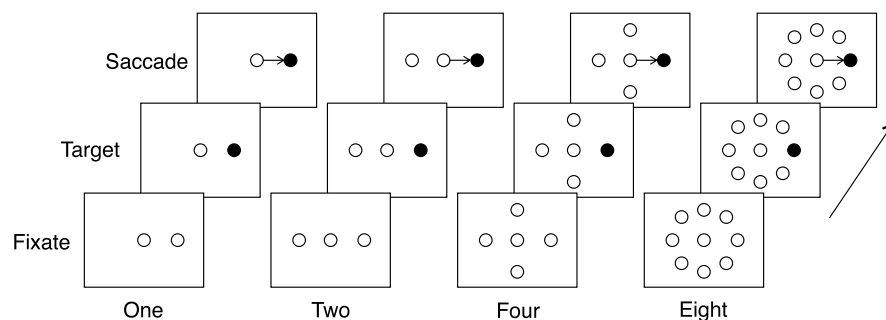

Figure 1. Center-out task. Monkeys completed separate blocks of trials on different days with one, two, four, or eight S–R alternatives. Each trial began when the monkey fixated a centrally located circle. After a variable period, a target appeared (pseudo-randomly for trials with two or more S–R alternatives), and monkeys responded by executing a saccade to the target location. Note that the placeholders remained "on screen" throughout each block of trials, and that the arrows depicted in the figure are for illustration purposes only.

occurred within ~90 ms of the target onset, or later than ~300 ms, or either the horizontal or vertical endpoint was more than 3 degrees from the median endpoint.

Each session began with a block of 100 practice trials in which the number of placeholders (i.e., 1, 2, 4, or 8) varied randomly from trial to trial. Following the practice block, for two of the monkeys (M1 and M3), the number of S–R alternatives remained constant within each session, and order across sessions was roughly counterbalanced. For the other two monkeys (M2 and M4), the number of S–R alternatives was held constant within blocks of 150 to 1000 trials, with order across sessions again roughly counterbalanced across monkeys. Neither the practice trials nor the first 100–200 trials of each block were included in the analysis of the data.

Because saccade latencies are known to vary systematically based on position (e.g., saccades to targets above the horizontal meridian tend to be faster than saccades to targets below the horizontal meridian; Heywood & Churcher, 1980), we compared saccade latencies for only those target locations that were used across the one, two, four, and eight S–R conditions. That is, target locations to the left and to the right of fixation along the horizontal meridian. For the one-target condition, monkeys completed separate sessions in which the target either appeared to the left of fixation or to the right of fixation, thus allowing this comparison.

Results and discussion

A one-way repeated measures ANOVA revealed that mean saccade RTs significantly *decreased* as the number of stimulus response (S–R) alternatives increased ($F(3, 9) = 11.9, p < .01$) (see Figure 2). The results of three planned comparisons (1 versus 2, 2 versus 4, and 4 versus 8 S–R alternatives) revealed that there was a significant decrease in RT between the 2 and the 4 S–R conditions ($t = 4.06, p < .01$) but not between the 1 and 2 S–R conditions ($t = 1.75, p > .10$) or the 4 and 8 S–R conditions ($t = 0.81, p > .40$). The decrease in RTs with S–R alternatives was highly consistent across individual monkeys (see Table 1), with one-way repeated measures ANOVAs, indicating a significant decrease in RT with an increase in S–R alternatives in each of the monkeys (all $ps < .0001$).

Carryover effects have been previously reported in saccade tasks. For example, humans and monkeys are slow to return their attention to a previously attended location (inhibition of return) (Dorris, Taylor, Klein, & Munoz, 1999; Posner and Cohen, 1984). In our paradigm, with two possible target locations, targets appear at the same location on consecutive trials ~50% of the time. With four possible target locations, this occurs only ~25% of the time. Thus, inhibition of return could explain longer saccade latencies on two target compared to four target conditions. To test this possibility, we removed trials in which the target appeared at the same location on
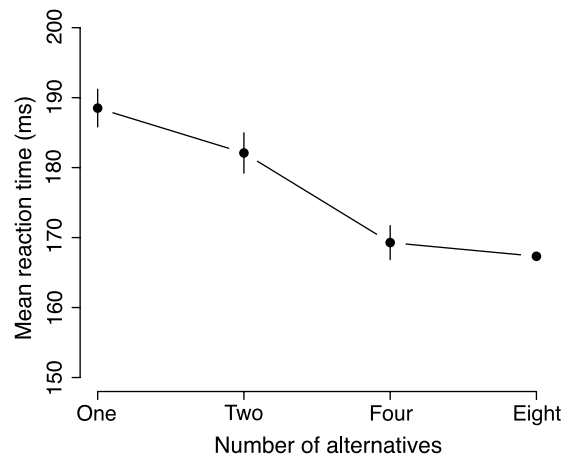

Figure 2. Experiment 1: results—monkeys. Mean RTs and standard errors (across participants) plotted as a function of S–R alternatives for Experiment 1 reveal that in monkeys saccade RTs decreased as a function of S–R alternatives.

consecutive trials. We, nevertheless, found a significant decrease in RT between the 2 and the 4 S–R conditions (182.6 ± 14.8 ms versus 168.3 ± 13.8 ms; $t = 4.23, p < .01$), indicating that the results of the present experiment cannot be explained by inhibition of return.

Thus, the results of Experiment 1 demonstrate that, at least in monkeys, saccade RTs decrease as the number of S–R alternatives increase. Because this effect is in the direction opposite that predicted by Hick, we term this effect an "anti-Hick's effect." It is possible, however, that this effect may characterize saccade RTs in monkeys, but not in humans.

Experiment 2

To determine whether the anti-Hick's effect found in monkeys generalizes to humans, we examined the effect of S–R alternatives on RT in humans.

Method

Nine students/employees of Washington University School of Medicine participated in the experiment (including authors—BML and LHS; ranging between 25–45 years of age). Stimuli were presented on a liquid crystal display (LCD). A chin rest (positioned 51 cm from the LCD monitor) was used to stabilize head position. Horizontal eye position was monitored using a scleral-reflectance eye movement monitor (Applied Science Laboratories, Model 210) mounted on an eye-glasses frame worn by the subject. The analog output of the eye-movement monitor was digitized at a rate of 1000 Hz. Other than the illumination from the LCD monitor, the experiment was conducted in a darkened room.

Response alternatives	1	2	4	8
Monkey (trials)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
M1 (3084)	174 ± 23	168 ± 22	146 ± 14.7	149 ± 18
M2 (3215)	250 ± 39	244 ± 35	228 ± 35.2	225 ± 34
M3 (1609)	184 ± 19	176 ± 17	169 ± 16.8	158 ± 12
M4 (1262)	158 ± 29	140 ± 22	137 ± 20.2	138 ± 22

Table 1. Mean reactions times (ms) for each monkey as a function of the number of response alternatives.

Subjects performed a "center-out" saccade task. A trial began when the subject fixated on a centrally located square appearing against a dark gray background. Surrounding the centrally located square were two or six white "placeholders."[1] The placeholders (1 × 1 degree), presented at 8 degrees of eccentricity, remained "on screen" throughout the block of trials and signaled the potential locations in which the target could appear. Following a constant delay (350 ms), a target appeared in one of the placeholders. The location of the target was pseudo-randomly selected such that the target location was randomly chosen on each trial, subject to the constraint that each target location occurred equally often within each block. Once the target appeared, subjects were instructed to execute a saccade to the target as quickly and as accurately as possible. An error message was shown to the subject and the trial discarded if the subject moved too early (saccade onset <100 ms), moved too late (saccade onset >400 ms), or did not move to within the target window (±5 degrees). On average, fewer than 5% of trials were aborted in either condition. The onset of an eye movement was defined as the point at which the velocity of the saccade exceeded 10°/s for at least 10 ms and subsequently exceeded 35°/s. Subjects completed three blocks of 60 trials with two placeholders, alternating with three blocks of 60 trials with six placeholders. Half of the subjects began with the two placeholder condition.

Results and discussion

The results of Experiment 2 reveal that, consistent with the results of Experiment 1, mean saccade RTs *decreased* as the number of S–R alternatives increased (see Figure 3). In particular, RTs decreased significantly from the 2 S–R (222.12 ± 1.67 ms) to the 6 S–R condition (212.12 ± 2.72 ms) ($t = 3.14$; $p < .01$). Thus, the results of this experiment reveal that humans, like monkeys, show an anti-Hick's effect for saccades directed to visual targets.

Experiment 3

It is possible that the increase in illumination associated with an increase in S–R alternatives resulted in the

decrease in RTs that we observed. Indeed, increasing the intensity (i.e., luminance) of a visual stimulus has been shown to decrease saccade RTs to such visual stimuli (for example, Bell, Meredith, Van Opstal, & Munoz, 2006; but see Darrien, Herd, Starling, Rosenberg, & Morrison, 2001). While the targets and placeholders were of equal luminance, it is possible that the increase in *overall* luminance associated with an increase in S–R alternatives resulted in a decrease in RT. In order to rule out this possibility, we removed the placeholders and repeated the earlier experiments.

Method

Six students/employees of Washington University School of Medicine participated in the experiment (including one author LHS; ranging between 25 and 45 years of age), as well as three adult male rhesus macaque monkeys (*M. mulatta*; including M1, M2, and M4 from Experiment 1).

The apparatus and procedure were the same as in Experiments 1 and 2, for monkeys and humans, respectively, with the exception that no placeholders were presented in Experiment 3. Because no placeholders were presented, humans were informed as to the number of S–R alternatives (2 or 6) prior to a block of trials, and monkeys
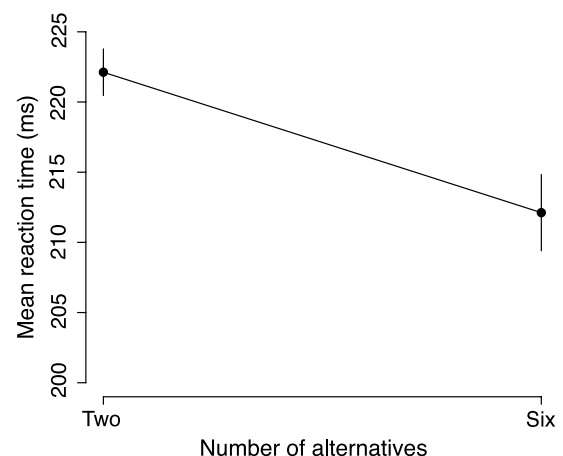

Figure 3. Experiment 2: results—humans. Mean RTs and standard errors plotted as a function of S–R alternatives for Experiment 2 reveal that in humans saccade RTs decreased as a function of S–R alternatives in humans as well as monkeys.

were practiced (150 trials) on a given number of S–R alternatives (1, 2, 4, or 8) prior to a block of trials.

Results and discussion

The results of Experiment 3 reveal that, consistent with the results of Experiments 1 and 2, saccade latencies *decreased* as the number of S–R alternatives increased in both monkeys and humans, respectively. In monkeys, a one-way repeated measures ANOVA on mean saccade latencies revealed that there was a significant main effect of stimulus–response alternatives ($F(3, 6) = 6.32$, $p < .05$). The results of three planned comparisons (1 versus 2, 2 versus 4, and 4 versus 8 S–R alternatives) revealed that there was a significant decrease in RT between the 2 (168.7 ± 16.1) versus 4 (158.0 ± 15.52) S–R conditions ($t = 3.54$, $p < .05$) but not between the 1 (167.7 ± 15.2) versus 2 S–R conditions ($t = 0.23$, $p > .80$) or between the 4 versus 8 (160.1 ± 15.30) S–R conditions ($t = 1.0$, $p > .30$). In humans, RTs decreased significantly ($t = 5.94$; $p < .0001$) from 2 (217.50 ± 1.77 ms) to 6 S–R alternatives (198.15 ± 2.74 ms) (see Figure 4). These results suggest that luminance was not a factor in determining the results of the previous experiments in both monkeys and humans.

Figure 4. Experiment 3: results—humans. Mean RTs and standard errors plotted as a function of S–R alternatives for Experiment 3 reveal that, as in Experiment 2, human saccade RTs decreased as a function of S–R alternatives.

General discussion

The results of the present experiments reveal the surprising finding that, in both monkeys and humans, saccade reaction time (RT) decreases as the number of stimulus response (S–R) alternatives increases. These results are in the direction opposite that predicted by Hick, and thus we term the effect an anti-Hick's effect.

The present results may seem counterintuitive unless considered in the framework of inhibition. In order to fixate a target, eye movements must be inhibited. In order to execute an eye movement, this inhibition must be overcome. We hypothesize that as the number of targets *decreases,* the propensity to any one particular target *increases,* thereby necessitating an increase in the inhibition required to prevent a premature saccade. When a saccade is eventually called for, additional time is required to overcome the increased inhibition, resulting in a delayed saccade onset and an anti-Hick's effect. We hypothesize that the neural correlates of the anti-Hick's effect would likely be found in the superior colliculus (SC), not only because it is involved both in inhibiting and triggering saccadic eye movements but also because the response of neurons in the SC is correlated with the number of potential saccade target locations (Basso & Wurtz, 1997). Future research in monkeys will be
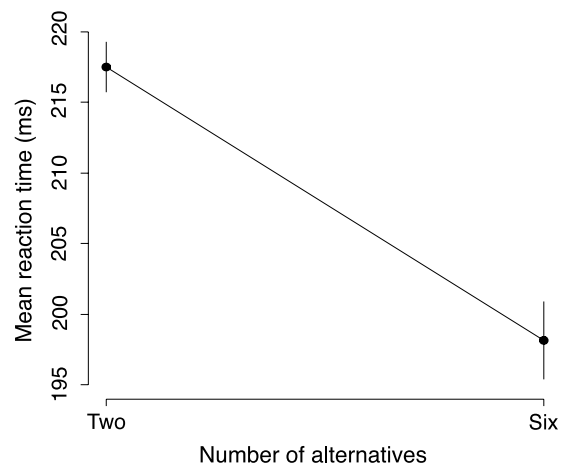
necessary to pinpoint the neural correlates of the anti-Hick's effect.

Why hasn't the anti-Hick's effect been reported previously in the literature? Differences in experimental paradigms may provide an explanation. Kveraga et al. (2002), for example, used a paradigm very similar to the present one, with the exception that the central fixation point was removed (leaving only the outline of the fixation point) simultaneously with the brightening of the peripheral target. The removal of the central fixation point may have resulted in the release of inhibition (similar to a "gap" effect; e.g., Bekkering, Pratt, & Abrams, 1996; Fisher & Ramsperger, 1984; Saslow, 1967), attenuating the anti-Hick's effect. The anti-Hick's effect is perhaps not entirely absent from their data—close inspection of their data reveals a trend toward an anti-Hick's effect in prosaccades (see Table 1 in Kveraga et al., 2002). Indeed, there appears to be a trend toward an anti-Hick's effect in saccadic latencies in several earlier published studies (see, for example, Heywood and Churcher, 1980; Morin and Forrin, 1965) as well.

The present results follow a tradition of examining the generalizability of Hick's Law (e.g., Kveraga et al., 2002; Longstreth et al., 1985; Wright, Marino, Belovsky, & Chubb, 2007) as well as other "laws" (see Adam, Mol, Pratt, & Fischer, 2006, for a violation of Fitts' Law). Factors such as practice, S–R compatibility, and effector selection have been hypothesized to influence the magnitude of the effect (Wright et al., 2007). Future research will be necessary to determine whether this effect generalizes to other experimental conditions (e.g., different stimulus configurations) as well as to other effectors (e.g., arm movements, but see Wright et al., 2007). The present results, however, are the first to suggest that the

relationship between S–R alternatives and RT may, at least for saccadic eye movements, be *opposite* that predicted by Hick.

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Footnote

[1]This choice of alternatives was chosen to maximize the number of trials. As in Experiment 1, only those target locations that were common across conditions (i.e., the locations to the left and right of fixation) were analyzed. Thus, as the number of potential target locations increases, the number of discarded trials also increases. In order to minimize the number of discarded trials, we used a condition with 6 as opposed to 8 S-R alternatives and analyzed only the horizontal saccades.

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