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Planning of saccadic eye movements

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Abstract Most theories of the programming of saccadic eye movements (SEM) agree that direction and amplitude are the two basic dimensions that are under control when an intended movement is planned. But they disagree over whether these two basic parameters are specified separately or in conjunction. We measured saccadic reaction time (SRT) in a situation where information about amplitude and direction of the required movement became available at different moments in time. The delivery of information about either direction or amplitude prior to another reduced duration of SRT demonstrated that direction and amplitude were specified separately rather than in conjunction or in a fixed serial order. All changes in SRT were quantitatively explained by a simple growth-process (accumulator) model according to which a movement starts when two separate neural activities, embodying the direction and amplitude programming, have both reached a constant threshold level of activity. Although, in isolation, the amplitude programming was faster than the direction programming, the situation reversed when two dimensions had to be specified at the same time. We conclude that beside the motor maps representing the desired final position of the eye or a fixed movement vector, another processing stage is required in which the basic parameters of SEM, direction and amplitude, are clearly separable.

completely specified before the movement begins. Direction and amplitude make up a minimal set of independent dimensions whose values determine the identities of all possible movements. One question that remains disputed is whether these two basic parameters of SEM, direction and amplitude, are specified separately or jointly in a unitary fashion. Neurophysiological explanations are usually inclined towards holistic models without any distinct computation of direction and amplitude values (Sparks, 1988). Neurons in the frontal eye fields and in the intermediate and deep layers of the superior colliculus, which activates immediately before the onset of a SEM (Robinson, 1972; Sparks, 1978; Lee, Rohrer, & Sparks, 1988; Sparks, 1988; Schall & Hanes, 1993), are arranged topographically to give rise to a motor map in which all movements are coded in terms of the desired final position of the eye or a fixed movement vector, not in separate terms of the direction and amplitude to be moved (Robinson, 1972; Glimcher & Sparks, 1992). A saccade is produced when the neurons at one location within the motor map become sufficiently active (Ottens, et al., 1984; Schall, 1995; Findlay & Walker, 1999).

However, it is questionable that completely specified motor programs exist for all possible SEM included in the motor map. It is also plausible that the motor map representing the desired final position of the eye is only one of the stages in the programming of an eye movement followed (or preceded) by some other stage(s) in which two basic parameters of SEM, direction and amplitude, are clearly separated from one another. Indeed, psychological data demonstrate that these two basic parameters of SEM are to a certain extent separable from one another. For example, the time required to reprogram a saccade in response to a pair of target displacements, followed one after another, depends on the spatial relations between these two displacements (Wheless et al., 1967). If the second displacement is in the opposite direction to the first target displacement, the latency of the response is about 40–50 ms longer than the average reaction time to a single displacement

Introduction

Saccadic eye movements (SEM) last only tens of milliseconds, which means that their parameters must be

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alone (Wheless et al., 1967; Komoda et al., 1973; Hallett & Lightstone, 1976; Hou & Fender, 1979). It was also shown that this extra time is required only if the new saccade is not in a direction similar to the canceled one. If directions of the new and previous saccade coincide and only its magnitude must be corrected, the reaction time could be even shorter than the average response time to a single displacement. These results seem to suggest that if one of the two parameters of the subsequent displacement remains unchanged there is no need to “rewrite” this part of the motor program. As a consequence, the response time to the second instruction will be shorter in proportion to the amount of time that is required to specify this particular parameter of the motor program. This means that programming direction and amplitude involve separate processes that can be manipulated independently from one another. Although this interpretation seems rather plausible it is still based on a rather intricate chain of inferences about how two subsequent responses, the canceled and the new one, interact with each other. It is also not the only possible way to explain the double-displacement data (cf. Ottes, van Gisbergen & Eggermont, 1984; Clark, 1999). Therefore, it is necessary to have a more straightforward method which allows the observation of preparatory processes that precede a single SEM.

One promising candidate is the movement precuing technique developed by Rosenbaum (1980). The basic idea of the precuing technique is to present an additional cue before the movement instruction, which gives information about some of the spatial parameters of the movement that must be executed on that trial. Regardless of the informativeness of the precue, the subject cannot produce the required response until the instruction is finally presented eliminating uncertainty about all parameters of movement. The major assumption of this method is that the subject uses the precued information to partially program upcoming movement before the instruction is presented. Comparing precued conditions with uncued ones (the former are typically shorter than the latter) it is possible to infer how much time it will take, on average, to specify values in the motor program that have been precued. Although the rationale of the precuing technique is rather simple and transparent, it has seldom been applied to the study of SEM planning. In one of the few studies in which the precuing technique was used, it was shown that subjects are faster in initiating saccades when they know either the direction or amplitude of the required movement in advance, compared with a condition without prior knowledge of the movement parameters required to execute (Abrams & Jonides, 1988). These results were interpreted as an indication that the direction and amplitude are specified separately, and not in a fixed serial order or in conjunction.

Beside obvious advantages the movement precuing technique also has some limitations. One of them is its static nature and failure to observe the actual time course of programming. However, in the end of his

seminal paper, Rosenbaum (1980) recommended, as an obvious extension of the precuing technique, to vary the delay between the precue and movement instruction. Unfortunately, as far as we know, nobody has proceeded in this promising direction. Another limitation of the precuing technique is the use of a separate cue in addition to the movement instruction itself. This means, in particular, that it is necessary to develop a separate explanation to the cue processing besides that of the model of motor programming itself. For example, it is well documented that an additional signal preceding the movement instruction can substantially reduce the response time even if it contains no specific information about parameters of the following movement (Saslow, 1967). In order to overcome or at least relax some of these limitations we developed a new method – the movement parameters disassociation technique – which can be considered as an extension of the precuing method.

The basic idea of this new method is to separate the programming of the direction and amplitude by presenting the information about their values separately at different time moments. For this purpose, the instruction about required SEM was not presented by indicating the exact location, as is customary in this type of experiment, but by presenting two symbols; the first indicating the direction in which to move and the second the distance through which the eye must move. Dividing the instruction between two separate signals allows them to be presented separately at different time moments with a certain Instruction Onset Asynchrony (IOA) between them. Presenting information about direction before amplitude, or vice versa, provides advance partial information and consequently extra time for preparation of the movement attribute that was presented earlier.

Another way to describe this method is in terms of response alternatives. Before presentation of either of the two signals the total number of alternatives is equal to the product of the number of potential directions and the number of potential amplitudes. After the presentation of the first signal the number of alternatives will be reduced by the factor equal to the number of alternatives values the first signal has. Thus, the experimental idea is to vary the time interval with the reduced number of response alternatives before the complete elimination of spatial uncertainty.

The most important advantage of this new method, over that of the static movement precuing technique, is that it allows the time course of programming to be observed. In this particular respect, this method is similar to the timed response paradigm (Schouten & Becker, 1967; Ghez, Hening & Favilla, 1990) which was invented for the disassociation of the mechanisms triggering movement initiation from those specifying response features. By instructing subjects to initiate responses in synchrony with temporally predictable signals and presenting information about required movement parameters at different times prior to response initiation, this task makes it possible to assess the course of visuomotor

preparation (cf. Ghez, Favilla, Ghilardi, Gordon, Bermejo & Pullman, 1997; Steglich, Heuer, Spijkers & Kleinsorge, 1999). Therefore, as we will demonstrate later, the examination of the time course of preparation considerably constrains the range of possible explanations. In particular, the deconstruction of programming time permits separation of the time needed to specify values under the motor program's control from the residual execution time, that is an irreducible time which is required to "translate" the program into executing movement commands. No other known method permits this separation. Another important difference from the precuing technique is the lack of an additional signal separate from the command signal itself: the required movement is fully specified and can be started if, and only if, both signals carrying information about SEM direction and amplitude are presented. Strictly speaking, there is no cue because both signals, irrespective of their presentation order, carry a part of the necessary information about parameters of the required SEM. This means, in particular, that eye movements studied by this method are not "reactive" in the sense that they are not triggered by an external event at the location where the eye must move to. Saccades in this type of experiment can be termed "volitional" because the subject intentionally selects a target from several alternatives on the basis of information carried by two separate instruction signals (for the distinction between "reactive" and "volitional" see: Findlay, 1981; Deubel, 1995).

Model of description

The preparation process for movement starts with the command signal onset and develops in time through different stages until an overt response can be registered. Some of these stages (e.g., the translation of the program into motor commands) are not likely to be influenced by the command signal and their total duration forms the signal-independent component of SRT. The complementary, signal-dependent SRT component can change as a function of the command signal, dependent on the IOA value. For simplicity we assume that these two SRT components are mutually independent random variables: $SRT = D(IOA) + R$, where D represents the signal-dependent and R the signal-independent (residual) component (cf. Dzhafarov, 1992 for nonindependent decomposition).

The major working assumption of the movement parameters disassociation technique is that the preparation process starts as soon as uncertainty about one of the two basic movement parameters, direction or amplitude, is eliminated. We are assuming that there are two separate neural preparatory activities embodying the direction and amplitude programming. The general way to represent these two preparatory activities is in terms of two separate growth-processes (cf. Dzhafarov, 1997). According to the growth-process models, the

elimination of uncertainty about either direction or amplitude of the intended movement starts a respective preparatory process that grows over time to reach a fixed threshold level. In general, these growth-processes are stochastic: even under exactly the same stimulus conditions it will take a different amount of time to reach the fixed threshold level of activation. For simplicity, however, we can assume that all growth-process trajectories can be sufficiently well approximated by linear functions (cf. Carpenter & Williams, 1995). One possible way that growth-processes are implemented is by accumulators that gradually build up their activity until they reach a fixed threshold level of activation.

In order to explain our data we proposed an extremely simple version of the growth-process models based on the following three assumptions:

- (1) A SEM can be initiated only after a fixed residual time interval R that has elapsed since two separate neural activities embodying the direction and amplitude programming have both reached a constant threshold activation level;
- (2) The rate at which neural activity grows toward the threshold level is approximately linear;
- (3) The growth-rate depends on whether these two growth-processes are taking place simultaneously or at different times: the growth-rate is slower when both direction and amplitude values have been specified concurrently than when only one is specified in isolation. There are two conditions when one of the two parameters can be specified in isolation: (a) the information about the second parameter is not presented yet or (b) there has been enough time to complete the programming of the second parameter.

In order to assist a better understanding of the proposed model, Figure 1 shows four linear growth-functions of direction and amplitude accumulators programmed either in isolation or in conjunction. The onset of the direction and amplitude instructions starts the respective growth-process. For example, after the elimination of uncertainty about amplitude value of upcoming SEM, it will take t_A milliseconds to complete amplitude programming, provided that the growth-process in the direction accumulator was not yet started or has already finished by reaching the threshold level activation. In turn, if both accumulators are active it will take t_{A*} msec to complete programming amplitude information. Analogously, t_D and t_{D*} are time intervals that are needed for the direction accumulator to reach the threshold when the other, the amplitude accumulator, is inactive or also growing respectively.

Figure 2 demonstrates two artificial examples. The first example (a) shows that at time t_1 the instruction about required amplitude is presented which initiates the growth-process in the amplitude accumulator A . Next, at time t_2 which is IOA ms after the first event, the direction instruction is presented which causes two actions: first, it initiates the growth-process in the

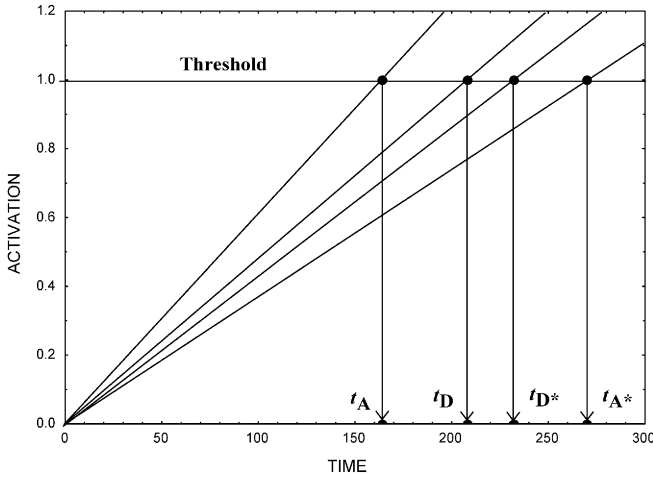


Fig. 1 Four linear growth-functions of activity in the direction and amplitude accumulators, provided that they are programmed either in isolation or in conjunction. t_A and t_{A^*} – time needed to reach the threshold for the amplitude programming in isolation and when the direction is also programmed respectively; t_D and t_{D^*} – time intervals that are needed for the direction accumulator to reach the threshold when the other, the amplitude accumulator, is inactive or it is also in a growing state

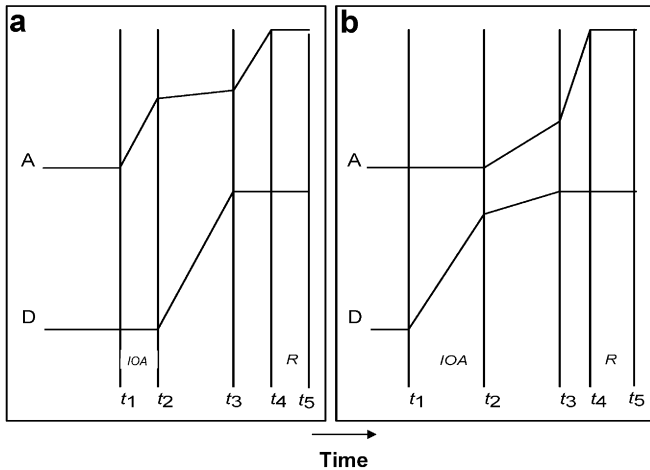


Fig. 2 Two hypothetical examples demonstrating the time course of the growth-processes in the amplitude (A) and direction (D) accumulators. (a) the instruction about required amplitude (t_1) was presented before the direction instruction (t_2) whose appearance temporarily slowed down the growth-rate in the amplitude accumulator until the programming of direction was finished (t_3). R is the residual time between the first observable external reaction (t_3) and the time moment then both growth-processes have reached the threshold. (b) The direction instruction is presented before the amplitude instruction. Until the presentation of the amplitude information (t_2), the growth-rate representing the direction programming is relatively fast and becomes sluggish with the start of amplitude programming. After reaching the threshold level activation (t_3) by the direction accumulator, the growth-rate of the amplitude accumulator increases and will take a relatively short time to reach its threshold level (t_4)

direction accumulator D and, second, slows down the growth-rate in the amplitude accumulator A. At time t_3 the growth-process in the direction accumulator reaches

the threshold which immediately releases the growth-rate in the amplitude accumulator which finally reaches the threshold at t_4 . After the residual time interval R at t_5 the overt movement can be detected. In the second example (b), the direction instruction is presented before the amplitude instruction. Until the presentation of the amplitude information (t_2), the growth-rate representing the direction programming is relatively fast but becomes sluggish with the onset of the amplitude programming. After reaching the threshold level activation (t_3) by the direction accumulator, the growth-rate of the amplitude accumulator increases and will take a relative short time to reach its threshold level (t_4). Following that moment some additional time R is needed before the onset of movement can be detected (t_5). In both cases, the predicted reaction time SRT is equal to $t_5 - t_2$, the time interval between the presentation of the second of two instructions and the time moment when R milliseconds, on average, have elapsed since the last of two growth-processes has reached the threshold level of activation.

Because it was assumed that the conjoint programming of direction and amplitude takes longer than their specification in isolation, the predicted SRT will obviously depend on the temporal overlap between two growth-processes being maximal at $IOA=0$ and decreasing with the diminishing of the overlap, that is with the increase of IOA leading to a Λ -shape of SRT versus IOA function.

For the prediction of the mean SRT from t , that is IOA , the following computation formula was used:

$$SRT(t) = t_A + R$$

$$\text{if}(t < -t_D)$$

$$SRT(t) = (1 - k_A)/k_D \cdot t + (1 - k_A) \cdot t_{D^*} + t_A + R$$

$$\text{if}(t \geq -t_D) \& (t < 0)$$

$$SRT(t) = -t + (1 - k_A) \cdot t_{D^*} + t_A + R$$

$$\text{if}(t \geq 0) \& (t \leq (t_{A^*} - t_{D^*}) \cdot k_A)$$

$$SRT(t) = -(1 - k_D)/k_A \cdot t + (1 - k_D) \cdot t_{A^*} + t_D + R$$

$$\text{if}(t > (t_{A^*} - t_{D^*}) \cdot k_A) \& (t \leq t_A)$$

$$SRT(t) = t_D + R$$

$$\text{if}(t > t_A)$$

Where t_D and t_A are times that are needed for the direction and amplitude accumulator respectively to reach the threshold when the other is inactive state and t_{D^*} and t_{A^*} are the same times when both accumulators are growing simultaneously; R is the residual time. For brevity, two ratios, $k_A = t_A/t_{A^*}$ and $k_D = t_D/t_{D^*}$, were introduced. Although the model contains five free parameters – two growth-processes with two different growth-rates plus the residual execution time R –, it is still restrictive, tolerating only a limited set of SRT versus IOA response-function configurations. Because of a simplifying assumption that all growth-rates are approximately linear, $SRT(t)$ function is described by no more than five successive linear segments.

Experiment 1

Methods

Subjects Three adult male subjects with normal uncorrected vision participated in the experiment. One of them was an author of this study and the others were naïve to the purposes of the experiments.

Procedure and apparatus Stimuli were generated on a monitor with 72 Hz vertical refresh rate by a PC. The observer had to change the fixation, as quickly as possible, from a central fixation point in the center of the screen to one of four equally probable new locations in two possible directions (left and right) at two different distances (4.6 and 9.2 degrees of visual angle) from the initial fixation point. Four potential refixation locations were marked by numerals, “1” and “2”, at shorter and longer distances respectively. These location marks with a size of 0.3° were permanently visible. Instructions specifying the required saccadic movement were presented around the central fixation point in the form of arrow heads (“<” or “>”) indicating left or right and a numeral (“1” or “2”) denoting the amplitude of the designated saccadic motion. The size of the symbols was 0.3° and they were exposed below and above the fixation point respectively with a 0.1° gap separating them from the fixation point. Both instructions, the arrow head and the numeral, were presented on the display screen simultaneously or in succession with plus-minus 42, 85, 128, 171, and 399 ms *IOA* between them. Throughout this paper the negative values of *IOA* correspond to the condition in which the direction instruction (arrow) was presented before the amplitude instruction (numeral, $D < A$). The positive values of *IOA* indicate that the amplitude instruction was presented before the direction instruction ($A < D$).

Each trial started when the subject fixated accurately on the central fixation mark. When the gaze deviated from the fixation point more than 1.8° the trial was delayed. The observer’s task was to move his eyes as quickly and accurately as possible to one of the four locations specified by the combination of the two instructions. Each trial did not end before the eyes had reached a distance no more than 1.8° away from the target or when the time limit of 2 s was exceeded.

Every experimental session consisted of series of 144-trial blocks with 12 repetitions in each condition (only $IOA = 0$ ms condition were presented 24 times). One block of trials lasted about 60 min. All conditions within a block were presented in random order. All subjects performed four blocks of trials in each of three sessions in which they participated. After each block, subjects were given a brief break.

Recording Observers were seated in a darkened room, in front of the monitor at a distance of 0.57 m. In eye movement experiments, the head of the subject is held in a fixed position by a bite bar. Eye movements were measured by an electromagnetic recording method with a scleral search ring (Alick, J., Rauk, M., & Luuk, A., 1981) warranting 1 ms temporal resolution via a 12-bit analog-to-digital converter with ca. 1-min spatial precision. The calibration was performed at the beginning of each session and was verified prior to each trial. If fixation systematically deviated from the expected value, then the calibration procedure was automatically repeated. Saccadic onset and offset were detected by an algorithm on the basis of velocity criteria. Trials on which the saccade latency was less than 80 ms and longer than 500 ms were discarded. Saccades in the wrong direction or with the wrong amplitude (the first landing was more than 1.8° away from the target) were also excluded from the further analysis. The overall error rate was 2.5%, 4.8%, and 5.8% for the subjects AL, HL, and JT, respectively.

Results

Figure 3 shows the mean SRT as a function of *IOA* for the three subjects. In general, the pattern of SRT change is similar for all three subjects: (1) For all three subjects, SRT has a maximum value when both instructions were presented simultaneously ($IOA = 0$); (2) The delivery of

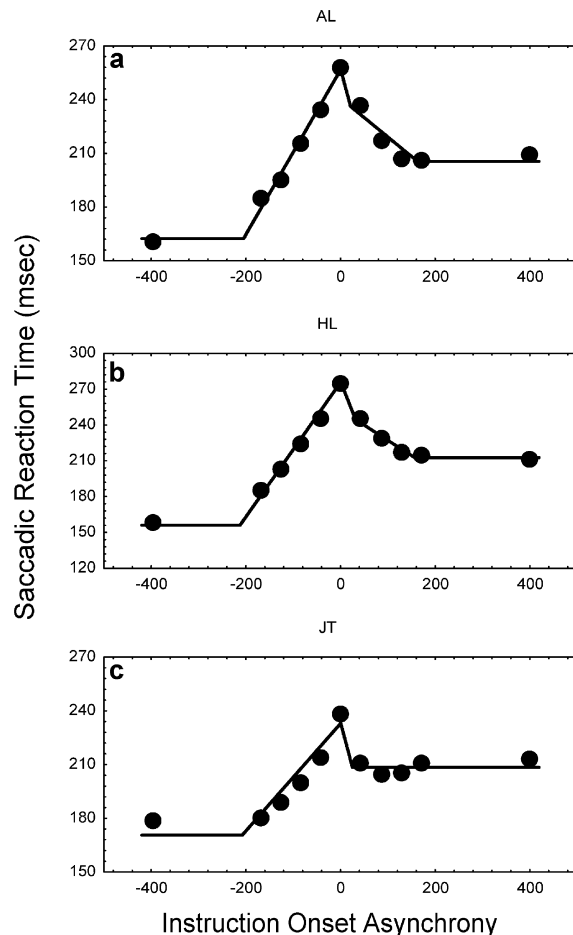


Fig. 3 The mean saccadic reaction time as a function of the *IOA* for three different observers, AL (A), HL (B), and JT (C). Each data point represent approximately an average of 400 trials. The mean standard error of data was smaller than that of the symbol size (see Table 1). The continuous curve is the best fitting function, whose numerical parameters are shown in Table 1

information either about direction or amplitude before the complete specification of the required movement reduced the duration of SRT; (3) The obtained SRT functions were highly asymmetrical: the benefit of presenting direction information before amplitude lasted longer and reduced SRT more than the benefit of presenting amplitude information before specifying direction. On average, SRT was about 40 ms shorter at extreme negative ($IOA = -399$) than at extreme positive ($IOA = 399$) values. This difference indicates that if only one of two parameters remains to be programmed (there was enough time to specify the other parameter presented in advance), then it will take less time to program amplitude than direction of the planned SEM. Data for all three subjects also contained a very rapid drop of SRT at small positive values of *IOA* (the amplitude instruction presented before the direction instruction) and slower decrease at larger positive values of *IOA* which indicates that the amplitude programming must be faster than the direction programming in isolation ($t_A < t_D$) and slower when two dimensions have to be specified simultaneously ($t_{A^*} > t_{D^*}$); Finally, (4)

the half-width of the AL-shape function (180–200 ms) was approximately equal or only slightly larger than the base-level, that is, to SRT measured at the largest negative values of IOA (–399 ms).

The best fit was found by an exhaustive search (a grid method) of all possible combinations of the model's five free parameters. The best fit in terms of the mean squared deviation is shown by continuous curves in Figure 3. Based on visual inspection, the fit was very good. This first impression was endorsed by a more rigorous comparison: the mean approximation error (the mean deviation of a data point from the best fitting function) was comparable to the mean standard error of data. The numerical values of the approximation together with the error values are presented in Table 1. The results of all three subjects indicate that the speeds of the direction and amplitude programming reverse their order when the shift from the isolated to simultaneous programming occurs. Quite surprisingly, for two subjects (AL and HL) the estimated residual time R was close to zero.

Figure 4 shows that it is very unlikely that changes in SRT were caused by the change in the duration of saccadic movement because the data of all three subjects were almost inseparable from one another. Figure 5 shows only the averaged saccade duration of the three subjects as a function of IOA separately for the two different movement amplitudes, 4.6° and 9.2°. Although SRT of the shorter jump was on average 13 ms longer, $t(5009) = 8.99$, $p < .001$, than SRT of the jump with the larger amplitude, there was no noticeable dissimilarity in their course of change with IOA.

The saccade amplitudes revealed a rather similar pattern: the mean amplitude of the first saccade towards the target was mainly independent of IOA (Figure 5). Saccades to the 4.6° targets were almost perfectly accurate (the mean was 4.7°) and identical for all IOA values, $F(10, 2449) = 0.86$; $p = 0.568$. However, saccades to more distant 9.2° targets were systematically undershot (the mean was 8.4°) and the analysis of variance demonstrates a significant effect of IOA, $F(10, 2456) = 2.27$; $p < .012$. The Sheffé test showed that only IOA = –399 ms (direction

Table 1 Parameter values of the best fitting functions shown in Fig. 3

Parameters	Subjects		
	AL	HL	JT
t_D	204	213	154
t_{D^*}	234 (30)	248 (35)	156 (2)
t_A	161	157	122
t_{A^*}	268 (107)	296 (139)	197 (75)
R	2	0	55
MAE	3.39	2.39	3.31
MSE	3.00	4.28	2.99

Note. t_D , t_{D^*} , t_A , t_{A^*} , and R – five parameters of the model (the best fitting values in milliseconds); MAE – the mean approximation Error: the mean deviation of a data point from the best fitting function (ms); MSE – the mean standard error of data (ms). In parentheses the increase of the growth-time, $t_{D^*} - t_D$ and $t_{A^*} - t_A$ respectively

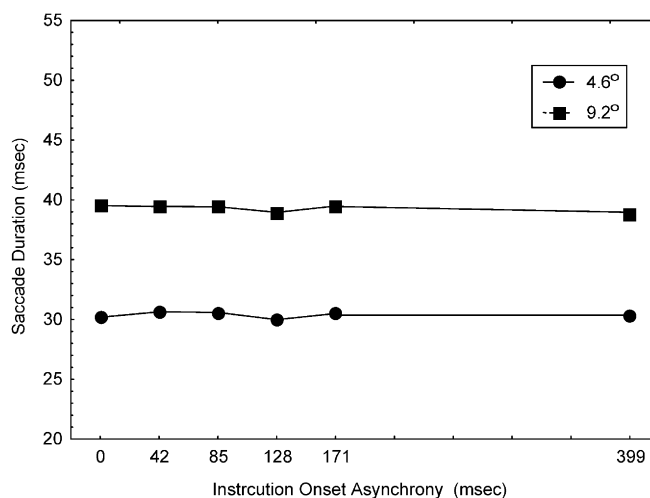


Fig. 4 The mean duration of saccadic movement as a function of IOA for two different amplitudes, 4.6° (●) and 9.2° (■)

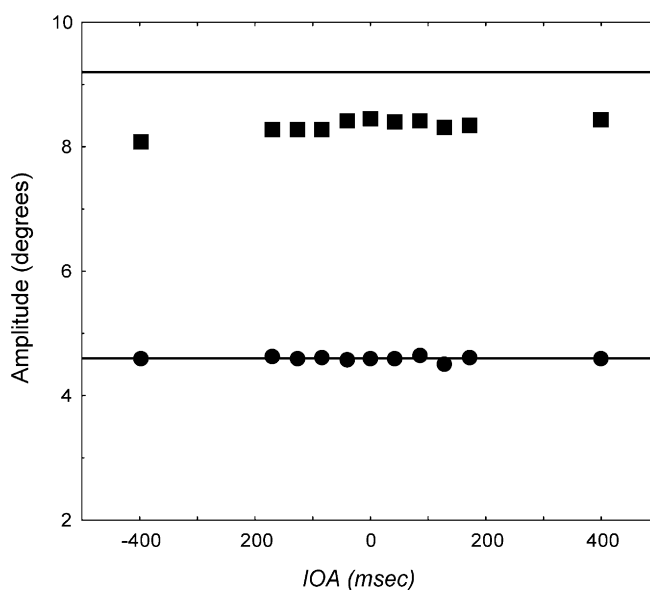


Fig. 5 The mean amplitude of the first saccade towards target at 4.6° (●) and 9.2° (■) from the fixation point as a function of IOA. Horizontal lines indicate the location of target. The standard error of means was 0.7° and 1.0° for the shorter and larger saccade amplitude respectively

information was known in advance) differed from several other asynchronies. However, this shortening of the saccade amplitude was modest and did not show a tendency for the eyes to land between two targets.

Discussion

Separate computation of saccade direction and amplitude

Our results undisputedly indicate that saccade amplitude and saccade angle can be prepared independently, not

necessarily in conjunction or in fixed serial order. The main argument supporting this conclusion is that the advanced partial information about either direction or amplitude reduced SRT. Abrams and Jonides (1988) also reported that saccades could be initiated faster when subjects knew either the direction or amplitude of the required movement in advance. They found that the preknowledge of direction or amplitude reduces SRT by about 13 ms compared with when neither direction nor amplitude are uniquely specified. Findlay and Walker (1999, pp. 671–672) write of Abrams and Jonides' results that they do not feel they are of sufficient magnitude (13 ms) to undermine their model, that is saccadic programming without separate specification of direction and amplitude. The reduction observed in this study is about 100 ms. One possible explanation of this discrepancy between our data and those reported by Abrams and Jonides may be an extremely high error rate (21%) in their study which probably resulted from a complicated stimulus-response mapping: in their experiment the stimulus indicating direction was opposite that of the required saccade.

Several previous studies using double-step target displacement paradigm have also reached the conclusion that direction and amplitude computations can be performed separately and in any order (Hou & Fender, 1979; Aslin & Shea, 1987). These results disagree with the conclusion reached by other investigators who found that there was a fixed hierarchical order in which the saccade parameters could be determined. In particular, it was proposed that the specification of amplitude can begin only after the direction decision has been completed (Komoda et al., 1973; Becker & Jürgens, 1979). Our data strongly support parallel nonordered programming of SEM parameters. In this respect it is encouraging that data about programming of manual movement are also consistent with the idea that different dimensions can be specified independently of one another, rather than in a fixed hierarchical order (Rosenbaum, 1980; Vidal, Bonnet & Macar, 1991; Gordon et al., 1994; Ghez et al., 1997). However, it remains for future studies to demonstrate whether parallel and serial programming are two alternative modes of processing which operate under different circumstances or whether there is only one operation mode. For example, Abrams and Jonides (1988) maintain that in some situations the saccade programming can be organized more holistically, solely in terms of the desired final location.

Interaction between direction and amplitude programming

The conclusion that the computation of saccade angle and amplitude involves separate mechanisms does not rule out the interaction between these two separate mechanisms. Indeed, the Λ -shape of the SRT function suggests that the two mechanisms interact with one another: the programming of either parameter is faster in

isolation than when both dimensions have to be specified at the same time. The same conclusion was reached by Aslin and Shea (1987) who maintained that “the direction decision mechanism interacts with the amplitude computation process” (p. 1939). However, methods used by previous studies did not determine the specific character of this interaction. The temporal disassociation paradigm goes beyond the previous studies by demonstrating that the interaction between direction and amplitude programming is highly asymmetric: the speed of amplitude programming deteriorates considerably more than the speed of direction programming in their conjoint programming condition (proportions in Fig. 1 correspond to actual average data). This asymmetry also indicates that the reduction of latency, by presenting the advance information, is not simply due to the decrease of the number of possible targets from four to two. Both the magnitude and speed of the latency reduction was very different depending on whether the advance information concerned direction or amplitude.

There are many possibilities that operationalize the described interaction that obviously exists between these two separate mechanisms. A description in terms of capacity limitation is one option. According to this interpretation, there is a central capacity to perform a limited number of different operations at the same time. When this limit is exceeded, the performance starts to decline. In the extreme case, time spent for the conjoint processing of two operations is equal to the sum of their processing times in isolation. In other words, one can ask whether specification times are additional (Rosenbaum 1980, p. 451). Let's suppose that it takes $t_D = 204$ ms to program direction and $t_A = 161$ ms amplitude for the forthcoming SEM in isolation (see Table 1, subject AL). From this it would be expected that, in the case of addition, 365 ms (i.e. $t_D + t_A$) will be needed to complete preparation for a forthcoming SEM when both movement attributes are processed simultaneously. In fact, the largest SRT value at $IOA = 0$ was only 258 ms, that is more than 100 ms less than could be expected from a completely serial processing mode. In fact, the drop in the processing speed was only about 14% for the direction processing and more substantial 66% for the amplitude processing, which is still considerably less from the doubling of the conjoint processing time. Data from the other two subjects demonstrate the same general pattern: the direction specification is affected very little by the specification of amplitude at the same time (only 1% drop for JT). This is contrary to the programming of amplitude which is much more vulnerable to the conjoint specification of parameters (88% slow-down for HL). Thus, the interaction between direction and amplitude specification mechanisms is clearly not additive.

With the exception of Abrams and Jonides (1988), who concluded that the times needed to specify direction and amplitude are approximately equal, it is typically believed that substantially more time is needed to specify direction than amplitude for both eye and manual

movement (Wheless et al., 1967; Megaw, 1972; Komoda et al., 1973; Rosenbaum, 1980). Neurophysiological data also demonstrate that providing information about movement direction shortens latency more than providing information about movement extent (Riehle & Requin, 1989). On the other hand, it was noticed that there is a state in the programming process after which the direction of the saccade cannot be changed but the magnitude can still be modified (see also Komoda et al., 1973; Hou & Fender, 1979; Becker & Jürgens, 1979) suggesting the possibility that amplitude specification can be more time-consuming. Results from this study provide a surprising solution to this apparent contradiction: there is no single answer to the question which one is faster, the direction or the amplitude programming! It depends on the circumstances. When either attribute, direction or amplitude, is specified in isolation it takes longer to specify direction than amplitude. However, the situation reverses when both dimensions have to be specified simultaneously: in that case it is faster to specify direction than amplitude. All previous theories of SEM programming have assumed, tacitly at least, that there is only one fixed rate with which movement attributes can be specified. The main advantage of the temporal disassociation method is that it allows relatively detailed inferences to be drawn about how the movement attributes are specified in isolation and conjunction. On the basis of our data, we can conclude that there are two different specification rates, one is operating when the attribute is programmed alone and the other when both attributes are programmed at the same time.

Contents of the growth-processes

In order to make the required movement, some preparatory activities are needed to specify an appropriate set of muscle commands before movement begins. These preparatory activities can be regarded as a plan for movement, that is “prescription for the values that a forthcoming movement should have on dimensions that are under the program’s control” (Rosenbaum, 1980, p. 446). The fact that partial advance preparation occurred for both dimensions suggests that there are indeed two distinct neural processes operating in parallel. As we proposed, these two separate preparatory activities can be described at an abstract level in terms of growth-processes. The most important characteristic of these two growth-processes is their steady increase in intensity over time until a fixed activity level is reached. What else beside the constant development rate can be said about these growth-processes? There is no doubt that the preparatory activity described by growth-processes includes a diverse set of psychological operations including perceptual operations that are required to recognize visually presented instructions, time needed for spatial attention to shift from one location to another, to load a movement program into a response buffer in working memory, and preparatory activity that

immediately precede muscle contractions. It also includes a certain amount of a general non-specific preparedness for movement, separate from specific programming activities, that was first described by Saslow (1967). By means of the temporal disassociation technique alone it is also impossible to distinguish between amount of time spent, for example, on the perceptual recognition or the construction of motor program in a narrow sense. For example, the observed asymmetry between programming of direction and amplitude, in isolation at least, may be entirely caused by a time difference that is needed to discriminate symbols indicating direction (“<” vs. “>”) and symbols specifying movement amplitude (“1” vs. “2”). Indeed, as can be observed in Table 1, t_D was 43, 56, and 32 ms larger than t_A for subjects AL, HL, and JT respectively. One obvious way to address this problem is to keep stimulation unchanged by modifying the task and required mode of response. For example, instead of moving the eyes the observer could be instructed to indicate which of the two symbols, “<” or “>”, was presented completely ignoring the presence of the second symbol, one of the two numerals. Comparing this discrimination task with another task in which two other symbols, “1” and “2”, are discriminated in turn, we can draw inferences about relative discriminability of these two pairs of symbols.

Experiment 2

This experiment was designed to address the question whether the asymmetric effect of advance information about movement direction and amplitude could be attributed to differences in instruction identification. If the differences between direction and amplitude programming are caused by time differences in the recognition of the instruction-symbols, it must be possible to obtain similar differences when exactly the same stimuli are used but eye movements are unnecessary. In other words, in this experiment we attempted to create a situation in which most of the motor requirements of the first experiment were eliminated but most of the instruction identification requirements were preserved (cf. Rosenbaum, 1980; Experiment 2).

Methods

Subjects Two of the subjects of the first experiment took part in this experiment as well. Unfortunately, the third subject was no longer available for the experiment. As recommended by one of the reviewers, we also included a control group of 6 naïve participants (4 men and 2 women).

Procedure and apparatus All stimulus conditions were identical to those of the first experiment. There were two different series. In the first series, the observer’s task was to indicate as fast as possible which of two arrow heads, “<” or “>”, was presented by pressing one of two buttons with the left or the right hand respectively. Subjects were instructed to ignore the appearance of the second irrelevant symbol, either “1” or “2”, before, at the same time as, or after, the arrow head. We have called this the arrow discrimination task. In the second series, the roles of the critical and irrelevant

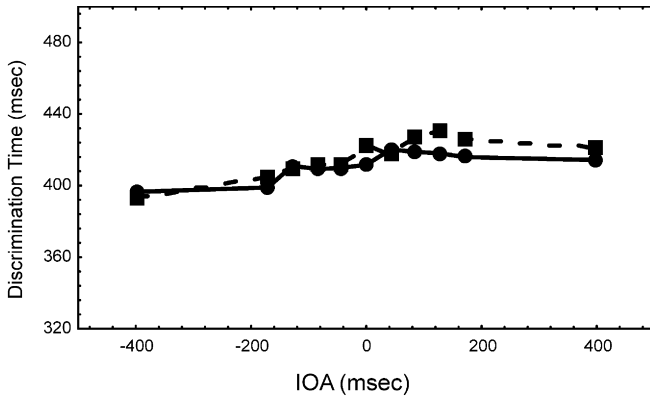


Fig. 6 The mean discrimination time of two symbols, arrows (●) or numerals (■), as a function of *SOA* for six naïve observers

symbols were reversed. The observer was told to discriminate numerals and to ignore the appearance of arrow-heads. This was the numeral discrimination task. Because manual reactions are slower than saccadic ones trials on which the response latency was less than 80 ms and longer than 1000 ms were discarded.

Results

The mean average reaction time of the control group as a function of *SOA* for both tasks is shown in Figure 6. There was practically no difference between processing numerals and arrows. The irrelevant stimulus preceding the critical one has affected the discrimination time with a slight tendency to reduce reaction time when it preceded the critical stimulus. However, this reduction was statistically insignificant. In any case, this reduction was considerably smaller and more spread in time than the effect of the partial preknowledge demonstrated in the first experiment. The results of subjects AL and HL were very similar to those shown for the control group in Figure 6.

Discussion

Do perceptual factors account for characteristics of SRT curves? Results of this experiment showed that latency characteristics of SRT curves, particularly their asymmetry, were not due to time difference in the discrimination of the instruction symbols. The reduction of SRT duration, due to delivery of information about either direction or amplitude before the complete specification of the required movement, cannot be explained by different encoding times of symbols specifying SEM direction and amplitude. In fact, the same conclusion can be reached from the inspection of SRT curves shown in Figure 3. Let us suppose that perceptual processing of arrow heads is more time consuming than processing of numerals. As a result of this, there will be a difference in time delay between the moment when the observer becomes aware of the direction and amplitude information, provided that both symbols were presented simultaneously. From the point of view of programming requirements, it is indif-

ferent whether this delay is caused by unequal perceptual processing time or the physical delay between presentation of two instructions. Thus, if there is a constant time difference in the processing of two types of instruction symbols, it should be notable in the SRT versus IOA curves: the maximum of the function will shift right or left from zero asynchrony depending on which of the two symbols has the longest processing time. Of course, the detectable shift is limited by the smallest IOA value that was used in the first two experiments. However, no such shift was seen in Figure 4: all three curves had their maximum at exactly IOA = 0. This observation, together with the results of the control experiment, suggest that perceptual factors alone do not account for the shape and the asymmetry of the SRT curves.

General discussion

Growth-process models

It is very gratifying that such a simple model with a limited number of free parameters was able to predict the change of reaction time as a function of IOA. According to the proposed explanation, the preparation of eye movement consists of separate decisions regarding relevant movement parameters, that is, direction and amplitude. A movement is initiated when both these separate preparatory decision processes reach a preset criterion level. Thus, our data strongly support the parallel distinctive-feature view of motor programming, rather than the serial hierarchical view, in these simple tasks at least.

One of the most universal ways to represent the decision process is with growth-processes that gradually build up their activity until reaching a fixed threshold-activation level. As an abstract construct, the growth-process may have many different interpretations in more meaningful psychological or physiological terms. For example, it is assumed that there is a steady flow of information about which of the many movement instructions is presented, providing support for a fixed accumulating rate (Carpenter & Williams, 1995). In turn, neurophysiological data show that many neurons related to SEM can be considered as accumulators building up their activity before movement starts. There is a consensus that the primary function of these accumulators is to make preparations for SEM (Hanes & Schall, 1996; Hanes et al., 1998; Schall & Thomson, 1999). For example, about one third of the saccade-related cells in the monkey SC began to build up their activity after the signal to make a SEM was presented and continue to discharge until the beginning of the SEM (Munoz & Wurtz, 1995a; Munoz & Wurtz, 1995b). As the number of possible targets decreases, the level of neuronal activity preceding the saccadic movement also increases (Dorris & Munoz, 1998; Basso & Wurtz, 1997, 1998). These buildup cells, which seem to be involved in the preparing, rather than in execution of SEM, are good candidates for accumulators that implement the

decision process about the required movement parameters.

Although the proposed explanation in terms of the growth-processes is more like applying a universal language of description, rather than developing a specific model, it allowed us to make precise quantitative predictions. It is important to notice that many other existing models of saccade generation are formulated either in the form of very general information flow-diagrams (e.g. Findlay & Walker, 1999) or as simulation networks (e.g. Clark, 1999; Trappenberg, Dorris, Munoz & Klein, 2001) which are able to reproduce some qualitative properties of SEM. Although more general and less restrictive models have their advantages, the approach that was taken in this study has its own distinction: we tried to build a formal model with a minimal number of parameters not specified in strictly quantitative terms. Three intuitively simple assumptions – separateness, linearity, and interaction – were sufficient to formulate the exact mathematical model which explains not only qualitative properties of SRT but the exact dependence of saccadic latencies from the change in IOA. The key assumption of the model is that separate decision processes are cross-talking with one another: the growth-rate in one decision process slows down when another decision process is active at the same time. In more meaningful terms, there is a central capacity to perform a limited number of different operations simultaneously. A surprising consequence of this mutual interference is the lack of a general answer to the question which of the two movement parameters, direction or amplitude, needs more time for specification. The specification time for direction is longer than that of amplitude in isolation, but shorter when both attributes are specified simultaneously.

In its present form, the proposed explanation is based on two obviously oversimplified assumptions. First, we assumed that the growth-rates of the decision processes were constant and could be approximated by linear functions. Second, we treated empirical data as deterministic, trying to predict only the mean reaction time. Obviously, to make the proposed model more realistic it is necessary to introduce some stochasticity. The most natural way of doing so, is to assume that the threshold criterion of the decision processes is not a fixed value but a random variable. Thus, all four decision times, to say nothing about the residual time R , are in fact stochastic parameters. Nevertheless, these limitations seem to constrain generality of our conclusions only marginally: a very broad class of stochastic growth-functions can be linearly approximated and there is no principal difficulties to extend model's predictions from the mean reaction time to higher order moments as well.

Temporal disassociation method

Without the proposed temporal disassociation method it was unthinkable to make detailed inferences about separate decision processes and their interactions. The

temporal disassociation method, as an elaboration of the movement precuing technique (Rosenbaum, 1983), allowed a considerably more specific assumption about movement initiation processes than has been possible before. As was mentioned, on the basis of the static precuing data it was concluded that the time to specify direction is generally longer than the time to specify amplitude. In the static precuing method the cue is typically presented long before all other movement parameters are specified. This means that there is enough time to process the precued attribute in isolation without interfering with the programming of other relevant characteristics of the planned movement. As we have demonstrated in this study, the time needed to specify a given movement parameter may be dramatically different depending on whether it is specified alone or simultaneously with other parameters. Thus, the main advantage of this new method is the possibility to look at the time course of programming. Another obvious advantage of the temporal disassociation method is the possibility for a direct estimation of the stimulus-independent residual time separate from the remaining stimulus-dependent portions of the reaction time. A comparison between SEM and hand movement, for example, revealed that the biggest difference between them was not in the speed of decisions but in the stimulus-independent residual time. One puzzling result was the extremely short residual times for two of three subjects in the eye movement experiment for which there appears to be no feasible explanation. It will remain to be investigated whether it is a technical approximation problem or a more fundamental difficulty which will necessitate the modification of the proposed model.

Representation of movement

This article was concerned with the problem of how relevant attributes of eye movements are specified prior to the time of their initiation. In this regard one of the basic questions remains: what aspects of movement are represented in the preparatory processes revealed by the temporal disassociation paradigm? Is the relatively holistic parameter like the final position or a more “analytic” representation in which parameters like direction and amplitude are kept apart? Both results of eye and manual movement suggested that different parameters of movement can be specified separately. This result seems to contrast with the growing popularity of holistic representations of SEM, according to which saccades are generated by the location of a peak in the two-dimensional salience map, representing the desired movement vector (Findlay & Walker, 1999). However, it seems that even holistic models relying on two-dimensional spatial maps cannot avoid the direction-amplitude separability problem. For example, Clark (1999) proposed a premotor explanation according to which the main variable component of saccadic latency is the time needed for spatial attention to shift from one location to another.

The next target selection is supposed to be executed by a winner-takes-all network which ‘disengages’ attention from the current location and ‘engages’ it at a new location. On the face of it, there seems to be no need to assume separate direction and amplitude programs and, perhaps, no need for any saccadic program at all. However, the winner-takes-all network operating on a retinotopic map cannot escape neither the fact that the saccadic system is capable of processing two movement concurrently (McPeck, Skavenski & Nakayama, 2000) nor the direction-amplitude separability problem as long as it concerns rapid transitions of spatial attention from one location to another. The question is whether attention moves along the shortest (or at least fixed) path connecting these two locations or whether there are multiple routes, which may indicate that direction and amplitude are in some way uncoupled. Indeed, Aslin and Shea (1987) demonstrated that following double-step target displacement the timing of the amplitude transition function and the angle transition function are not coincident. They found that the angle transition function occurred at a consistent time prior to the initial saccade, whereas the amplitude transition function occurred at a variable time prior to the initial saccade, indicating that these two transition functions are disassociated. Thus, provided that these results can be described in terms of spatial attention, it is unavoidable to represent the direction and amplitude as two separate attributes of the retinotopic representation. Even a strict coupling between visual attention and saccade programming (cf. Rizzolatti, Riggio, Dascola & Umiltà, 1987; Deubel & Schneider, 1996) does not exclude that direction and amplitude could be separable. Also, from a logical point of view it is necessary that at one stage of movement preparation, the desired final position for the next fixation will be translated into a “language” which is understandable in terms of motor commands: which direction and what distance to rotate the eyeball. In other words, these two representations, holistically and analytical, are not necessarily incompatible but may simply represent different stages in the movement preparatory process. Neurophysiological data also indicate the existence of distinct levels of signal processing from the general (“movements”) to the highly specific (“muscles”) (Riehle, 1991; Alexander & Crutcher, 1990; Kakei, Hoffman & Strick, 1999).

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