

RESEARCH ARTICLE

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Discrete and continuous planning of hand movements and isometric force trajectories

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Abstract We have previously demonstrated that, in preparing themselves to aim voluntary impulses of isometric elbow force to unpredictable targets, subjects selected default values for amplitude and direction according the range of targets that they expected. Once a specific target appeared, subjects specified amplitude and direction through parallel processes. Amplitude was specified continuously from an average or central default; direction was specified stochastically from one of the target directions. Using the same timed response paradigm, we now report three experiments to examine how the time available for processing target information influences trajectory characteristics in two-degree-of-freedom forces and multijoint movements. We first sought to determine whether the specification of force direction could also take the form of a discrete stochastic process in pulses of wrist muscle force, where direction can vary continuously. With four equiprobable targets (two force amplitudes in each of two directions separated by 22° or 90°), amplitude was specified from a central default value for both narrow and wide target separations as a continuous variable. Direction, however, remained specified as a discrete variable for wide target separations. For narrow tar-

get separations, the directional distribution of default responses suggested the presence of both discrete and central values. We next examined point-to-point movements in a multijoint planar hand movement task with targets at two distances and two directions but at five directional separations (from 30° to 150° separation). We found that extent was again specified continuously from a central default. Direction was specified discretely from alternative default directions when target separation was wide and continuously from a central default when separation was narrow. The specification of both extent and direction evolved over a 200-ms time period beginning about 100 ms after target presentation. As in elbow force pulses, extent was specified progressively in both correct and wrong direction responses through a progressive improvement in the scaling of acceleration and velocity peaks to the target. On the other hand, movement time and hand path straightness did not change significantly in the course of specification. Thus, the specification of movement time and linearity, global features of the trajectories, are given priority over the specific values of extent and direction. In a third experiment, we varied the distances between unidirectional target pairs and found that movement extent is specified discretely, like direction, when the disparity in distances is large. The implications of these findings for contextual effects on trajectory planning are discussed. The independence of extent and direction specification and the prior setting of response duration and straightness provide critical support for the hypothesis that point-to-point movements are planned vectorially.

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Introduction

Purpose, context and experience achieved through practice in particular tasks are crucial to how we perceive and respond to sensory stimuli (Evarts et al. 1984). In planning movements to visual targets, differences in contex-

tual information or instruction allows subjects to “prepare” different features and particular parameters of motor responses. For example, information provided to an animal to respond in a particular way to proprioceptive (Evarts and Tanji 1976) or visual stimuli (Martin and Ghez 1985; Alexander and Crutcher 1990a–c; Martin and Ghez 1991; Riehle 1991) determines whether short-latency task-related activity evoked in motor cortex neurons is facilitated or suppressed. Similarly, directional precues produce set-related discharges of neurons in lateral premotor areas of monkeys (Riehle and Requin 1989). However, it is often difficult to distinguish which response features are programmed in advance and which are programmed during the interval between stimulus and response.

In a previous series of studies we introduced a timed-response task to dissociate the mechanisms triggering movement initiation from those specifying response features and focused on relatively simple elbow force trajectories (for review see Ghez et al. 1990). By instructing subjects to initiate responses in synchrony with a temporally predictable auditory cue and presenting visual targets at different times prior to response initiation, this task makes it possible to assess the time course of visuomotor processing. Those studies showed that before specific information about a randomly varied target is available, subjects set default values for amplitude and direction based on expectation. Then, after the target is presented specification evolves progressively over a 200 ms or more. In the case of amplitude, the default is set in the middle of the target range and specification occurs through a progressive improvement in scaling of the speed and acceleration of force development (Henning et al. 1988a). For direction, the default is instead selected discretely as extension or flexion. Specification takes the form of a progressive reduction in the proportion of directional errors – a stochastic rather than a continuous process (Favilla et al. 1989). Interestingly, we found that amplitude is specified progressively for both correct and wrong direction responses. Correspondingly, biases in the distribution of target amplitude probability in a single direction produced biases in response amplitude for both (Favilla et al. 1990b). Thus, in elbow force pulses, the preparation and specification of extent and direction were both organized in parallel. The present experiments were undertaken to extend those observations to forces and movements evolving in a two-dimensional space.

Two considerations limit the application of our earlier observations to more spatially complex force responses or to movements with multiple joint motions. First, the parallel specification of amplitude and direction might have reflected the discrete quality of force direction at the elbow, a two-valued variable which can only be either flexor or extensor. In fact, it might have simply been the product of our measurement system which monitored force in only those two exclusive directions. On the other hand the discrete mode of specification could have reflected a specific strategy which subjects might adopt in

other contexts as well, and serve some particular advantage or optimization. The findings of Ottes et al. (1984) provide an example of this in ocular saccades. Those authors demonstrated that at wide target separations, short-latency saccades are directed randomly towards one or the other of two alternate target locations when separation is great and to an average location when separation is small. A plausible hypothesis would therefore be that subjects adopted a discrete strategy to increase the number of successful responses while minimizing trajectory corrections. Since in aimed force pulses the ability to extend force rise time is limited (Gordon and Ghez 1987a), the use of a discrete strategy might be a strategic adaptation to reach the correct target in at least some responses.

A second difficulty in extending our earlier results to the more general case of point-to-point movements with motions at multiple joints is biomechanical: in multijoint movements, extent and direction at the hand are not independent at either the joint or the muscle level. Errors in activating agonist or antagonist muscles at any proximal joint will result in directional errors at the hand. Additionally, because limb inertia is anisotropic (Hogan 1985), for a target at constant distance, movement duration needs to be reduced for movement directions in which inertial resistance is low (typically along the axis of the forearm) to avoid overshooting the target and vice versa (Ghez et al. 1990; Gordon et al. 1994a). Similarly, unless taken into account in the commands to muscles, dynamic interactions among linked segments would distort limb trajectories intended to be straight and produce large movement errors (Hollerbach and Flash 1982; Ghez and Sainburg 1995; Sainburg et al. 1995).

The present study reports three experiments in which we used the timed response paradigm to address these unresolved issues. In the *first experiment*, we sought to determine whether at the wrist the specification of response direction could also take the form of a stochastic process from discrete default values. At this joint, direction can vary continuously throughout the two dimensions of flexion-extension and radial-ulnar deviation. As at the elbow, force direction remained specified as a discrete variable for both narrow and wide target separations whereas force amplitude was specified continuously. However, relatively high response variability precluded a detailed analysis of response trajectories. In the *second experiment*, we analyzed the time course of direction and extent specification in a multijoint planar hand movement task where subjects show greater accuracy. Those results showed that direction may be specified continuously or discretely depending on the disparity of target directions. Like elbow force pulses, extent specification occurs concurrently with direction, and through progressive improvement in scaling rather by extension of movement duration. Finally, in the *third experiment* we examined whether movement extent can be specified discretely when the separation of alternative distances between targets is large.

Preliminary accounts of this work have appeared in abstract form (Bermejo et al. 1989; Favilla et al. 1990a).

Materials and methods

Subjects

Subjects were eight neurologically normal right-handed adults (six men and two women, aged 27–41 years). Four subjects participated in experiment 1 (wrist force pulses). Five subjects participated in experiment 2 (directional specification of hand movements); four of these also participated in experiment 3. In experiments 1 and 2, two subjects were naive to the purpose of the study while others were co-authors; in experiment 3 only one was naive. All were familiar with the tasks, having received two or more sessions of practice aiming hand movements or force pulses to targets displayed on a screen in the timed response paradigm. All subjects signed an informed consent form conforming to the requirements of the Columbia Presbyterian Medical Center and Research Foundation for Mental Hygiene Institutional Review Boards.

Apparatus

Force pulses (experiment 1)

Subjects were seated with their upper arm vertical, their elbow flexed at 90° and their forearm and hand in a padded aluminum restraining device mounted on a horizontal support surface at waist level. The forearm was in a neutral position of supination-pronation such that the palm faced medially. An isometric manipulandum immobilized the wrist and hand and held the fingers in a comfortable semi-extended position. Two custom-designed strain gauge systems, centered at the axis of rotation of the wrist, were used to record the forces developed around the wrist in the flexor-extensor direction and in the ulnar-radial direction.

The signals from the strain gauges were amplified and, following analog to digital conversion, acquired on a Macintosh computer which controlled the experiments. The subjects faced an oscilloscope screen (24 cm × 19 cm, Kikusui) whose single beam was controlled along the horizontal and vertical axes by signals from the two force sensors. The spatial correspondences between force display and the directions of the force produced by the subjects were highly compatible and cross-talk was minimal: flexor force, involving pushing medially on the strain gauge, produced a medial deflection of the beam, whereas extension produced a lateral deflection but not vertical motion. Radially directed forces, involving upward forces at the hand, were displayed vertically upward on the screen whereas ulnar forces were downward. Zero net force was displayed in the center of the screen. Four yellow light emitting diodes (LEDs), taped directly on the face of the oscilloscope screen, indicated the locations of force targets.

Planar hand movements (experiments 2 and 3)

The apparatus used here has been described previously (Gordon et al. 1994b). Seated subjects, facing a computer screen (17 cm × 12 cm) at eye level, moved a hand-held cursor on a digitizing tablet (42 cm × 30 cm, resolution 0.0025 cm, Numonics model 2200) located at waist level. At the initial position, prior to movement, the upper arm was approximately vertical and the forearm approximately horizontal. Wrist movements were restricted by a cast.

The position of the hand-held cursor on the tablet (x and y coordinates) was sampled by a Macintosh computer at a constant rate of 200 Hz and was displayed on the computer monitor with a reduced gain ($2.4 = 1$) as a screen cursor. Vision of the hand and arm was blocked by a drape.

Tasks

For both force impulses and hand movements subjects performed the timed-response paradigm as described previously (Hening et

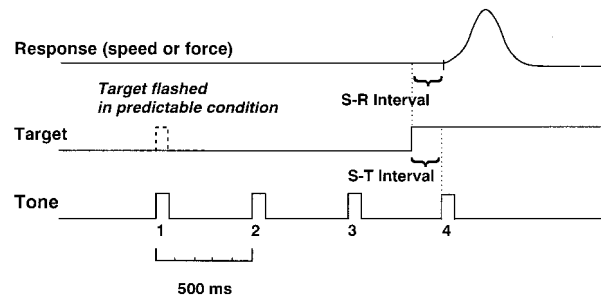


Fig. 1 Timed response paradigm. Subjects were trained to initiate a force pulse or movement (*top trace*) in synchrony with the last of a regular series of four tones (*bottom trace*). The target is displayed at a variable and unpredictable time prior to the fourth tone (S-T interval). The actual time between target presentation and response onset is called the S-R interval. In the predictable condition, the target is precued by briefly displaying it at the time of the first tone

al. 1988a) (Fig. 1). This task required the subjects to attend to two demands concurrently: to initiate a response *in synchrony* with the last in a series of four successive 75-ms tones (ca 60 dB; interstimulus interval 500 ms) presented through earphones, and to *aim their response to a target*, presented visually at an unpredictable time prior to the fourth tone (or S-T interval). Variations in stimulus-tone (S-T) interval resulted in differences in the time between target presentation and response onset, referred to as S-R interval. The latter was assumed to reflect the time available for processing target information. The amount of information processed in this interval was varied across blocks by either precuing the upcoming target (*predictable condition*) or not (*unpredictable condition*). Although subjects had no difficulty performing this dual task with predictable targets, when targets were unpredictable they frequently delayed response initiation (Hening et al. 1988a), producing more responses at long than at short S-R intervals. This strategy was minimized in experiments 2 and 3 by displaying explicit information about timing errors on the computer monitor after each trial and encouraging subjects to minimize this.

Experiment 1

Targets were in one of four possible target locations requiring either 15 N or 7.5 N in either of two directions from a common point at zero wrist force. For convenience, the two directions are described here with reference to the direction of simple wrist flexion. Force directions deviating from the target direction radially or clockwise are referred to as positive. The two target directions required subjects to produce forces combining wrist flexion with either ulnar or radial deviation at two directional separations of 22° and 90°.

Trials began when wrist forces were within narrow windows around zero for both force axes. After a random interval of alignment, the sequence of tones began and, between the third and fourth tones, one of the four LEDs was lit. Subjects were instructed to produce "a single, uncorrected pulse of force whose peak is as close as possible to the target." In the *predictable condition* the upcoming target LED was turned on transiently for 200 ms with the presentation of the first tone. In the *unpredictable condition*, all LEDs were transiently lit at that time. In both conditions, subjects had continuous visual feedback of the force display and were encouraged to be as accurate as possible. As in previous studies of similar force pulses generated at the elbow (Hening et al. 1988a) or at the metacarpophalangeal joint of the index finger Hening et al. 1988b), subjects were trained over two or more sessions prior to the actual experiments to produce smoothly rising forces without inflections indicative of purposeful corrections. Experiments were comprised of four blocks of 40 trials each. Within blocks,

targets were either all predictable or all unpredictable. Successive blocks were presented in an A-B-A-B sequence.

Experiment 2

Four possible targets, located at two distances (3.2 and 9.6 cm) in each of two directions from a common origin, were presented to the subjects. The two directions were symmetrically arrayed around the vertical axis on the screen. Upward targets on the screen corresponded to the straight-ahead direction. For convenience in describing the results we defined this as 0° , and clockwise angles were considered negative. The five pairs of target directions were symmetrical with respect to this 0° axis and were separated by 30° , 60° , 90° , 120° and 150° (see Fig. 7). The order in which these targets were presented and the time at which they were presented within the third and fourth tones were both randomized.

Experiment 3

In this case there were only two alternative targets in each block of trials rather than four. These targets were located along the -60° line at two distances from a common starting position. Targets were either at 3.2 and 9.6 cm, 3.2 and 19.2 cm, 3.2 and 38.4 cm or 1.6 and 38.4 cm, corresponding to distance ratios of 1:3, 1:6, 1:12, 1:24. These targets were again presented in a randomized order and at random times between the third and fourth tones. Because there were only two, the same target could be presented on several consecutive trials.

In both experiments 2 and 3, targets were presented in four blocks of 64 trials in which each of the four targets was present 16 times, twice at each of eight S-T intervals (33.3, 66.7, 100, 133.3, 200, 266.7, 333.3, 400 ms). Target shifts were predictable in the first block and unpredictable in the following three blocks. About 5 s of rest were allowed between trials and 2 min between blocks.

At the start of the trial, cursor position on the tablet was displayed on the computer monitor together with circles representing the starting position and the four the possible target locations. Subjects were to position the screen cursor inside the start circle when the series of four auditory tones was presented. The target for the particular movement was displayed at varying times (0–400 ms) before the fourth tone, by being reversed from white to black. Subjects were to make a “single, quick, uncorrected movement” to the target and to initiate this movement in synchrony with the fourth tone. The screen cursor was blanked at the time of the fourth tone to prevent subjects from using visual information to correct their trajectory. In the *predictable condition*, the target was precued by being presented briefly for 200 ms with the first tone, 2 s before movement initiation, as shown in Fig. 1. In the *unpredictable condition*, the visual target appeared only between the third and the fourth tones at varying times.

In order to help subjects be both spatially and temporally accurate, they were provided with the following information after each movement: (1) a screen display of their hand path, (2) a screen display of their timing error; (3) a cumulative performance score.

Data analysis

Details of the data analysis procedures were as described in previous studies of force pulses (Ghez and Gordon 1987; Gordon and Ghez 1987a; Hening et al. 1988a; Favilla et al. 1989) and planar hand movements (Gordon et al. 1994b). Briefly, after smoothing the data into polar coordinates and computed first and second time derivatives for both force and position amplitudes. Movement onsets, peak values of force and position derivatives as well as movement endpoints were marked by automatic computer programs. These critical points were always checked using path and time series displays and corrected when necessary. Responses showing more than one peak in the velocity profile or those with evident changes

in direction were assumed to show voluntary corrections and were rejected from analysis. The percentage of rejected trials was below 5% in all sessions and subjects.

We computed two path shape indices. One was an index of path curvature, represented by the angular difference between the direction of the vectors from start to endpoint, and from start to the hand location at the time of the peak acceleration. The other was the linearity index of Atkeson and Hollerbach (1985), which is used more commonly (e.g., Georgopoulos and Massey 1988; Jakobson and Goodale 1989; Smit and Van Gisbergen 1990). This consists of the ratio of the largest distance on the hand path to a straight line drawn from start and end point, to the linear distance between start and end-point. S-R interval, the time between target presentation and response onset, was computed for each response as was timing error (the difference between the tone onset – the required time – and actual onset time of response initiation).

The spatial distributions of end points were plotted and means and standard deviations of trajectory parameters from individual subjects were computed on data grouped into successive S-R interval bins. Because of the greater variability of force than of positional trajectories, and because of the paucity of data in certain time bins, data were grouped across subjects (see Results) in experiment 1. Lines were fitted to the points of scatter plots of timing data using a nonparametric curve-fitting procedure called LOWESS, or locally weighted scatterplot smoother (Cleveland 1979).

Results

Experiment 1. Direction can be specified discretely in two-dimensional force space

Within two sessions of practice subjects were able to produce force impulses whose mean peak amplitudes and directions matched those required by precued targets. Figure 2A shows overplots of representative force paths produced by a subject aiming forces to precued targets at 90° separation in one experiment. Force paths are straight over

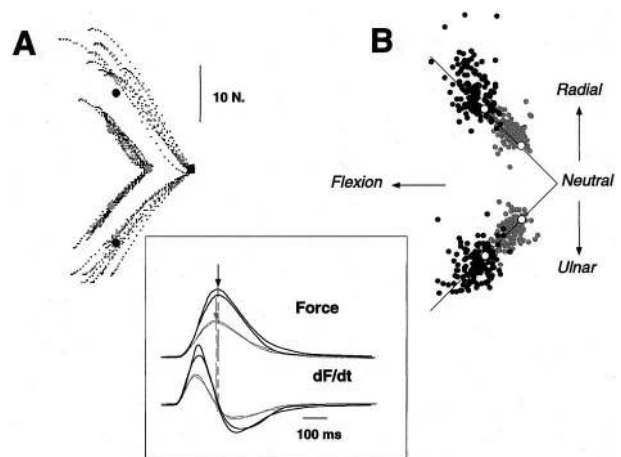
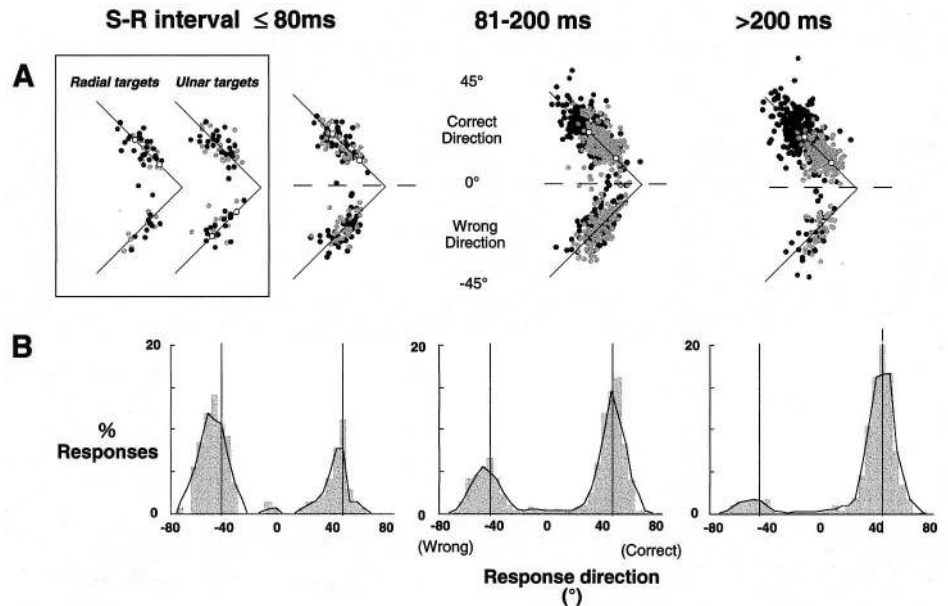


Fig. 2A, B Experiment 1. Force paths and peak forces by one subject to each of four targets in the predictable condition. Target separation is 90° . **A** Force paths to low force targets (7.5 N) are in gray and those to high force targets (15 N) are in black. **B** Peak forces are plotted as small circles. Those to low force target are gray and those to high force target are black. **Inset:** Ensemble-averaged force and dF/dt for responses to each target are superimposed. Those to small targets are displayed as dotted lines, while those to large targets are displayed as continuous lines. Averages are synchronized at force onset

Fig. 3A, B Experiment 1. Responses by all subjects to unpredictable targets with 90° separation divided into three S-R intervals. **A** Peak forces to each of the four targets. Those to the small targets are *gray*. *Inset*: Responses to the radial and ulnar targets are displayed separately for S-R interval ≤ 80 ms. In the plots to the *right* of the inset, correct direction responses are displayed as though all were in the radial (upward) direction, while wrong direction responses are displayed as though they were all in the ulnar (downward) direction. **B** In *gray*, histograms of force directions measured at the time of the peak dF/dt for the three S-R intervals are fitted with a LOWESS line (see Materials and methods). *Vertical lines* indicate the two target directions



most of their course and oriented along the 90° direction, indicating reasonably accurate preplanning of force direction. Peak forces were, however, frequently overshoot, as noted in our earlier studies of finger (Hening et al. 1988b) and elbow force impulses (Hening et al. 1988a). Nevertheless, ensemble averages of force trajectories (boxed inset in Fig. 2) show that the peak rate of change of force scales with peak force indicating preplanning of force magnitude as well (Ghez and Vicario 1978b; Gordon and Ghez 1987a). Responses to the other pair of targets were similar. While the range of force rise times varied from 93 to 135 ms in different subjects, it did not vary significantly with peak force. In all subjects variation in dF/dt accounted for over 90% of variance in peak force. The grouped distributions of peak forces around the four targets, in Fig. 2B, shows the overall spatial accuracy of these responses for responses to predictable targets.

When targets were unpredictable, the spatial dispersion of peak forces became dependent on S-R interval, that is, on the time available for processing target information. The spatial distributions of responses initiated within three S-R interval ranges are plotted in Fig. 3A. Data across subjects were grouped to increase the numbers of responses within each interval; however, when enough points were available, the trends were similar for individual subjects.

The box on the left shows overplots of responses to the two radial and ulnar targets separately for the shortest S-R interval (≤ 80 ms). For both target directions there were two separate clusters of points. One cluster was along the correct direction axis while the other was along the wrong direction axis¹. Since this trend is the

same for the two target directions, we combined them (overlying radial and ulnar targets) to distinguish correct from wrong direction responses. Figure 3A shows that the proportion of responses along the wrong direction axis diminishes in successive time bins. In order to evaluate the initially programmed direction we measured response directions at the peak dF/dt (Gordon and Ghez 1987b). The resulting directional distributions are plotted in Fig. 3B. At S-R intervals of 80 ms or less, directions are distributed bimodally, with peaks around the direction of the target, both for correct and wrong direction responses. In successive time bins the wrong-direction peak becomes progressively smaller and by 200–300 ms it represents only about 11% of responses.

Figure 3A shows that in the earliest interval (≤ 80 ms), responses to the small and large force targets overlap (gray and black points) for both correct and wrong directions. In the next two intervals, however, correct direction responses to the two force targets separate progressively, and for S-R intervals ≥ 200 ms, the distributions resemble those shown in Fig. 2B for predictable targets (note the similar tendency for systematic overshooting). A progressive trend for amplitude specification is not apparent among wrong direction responses. Whether this was related to the smaller number of responses or to the fact that subjects curtailed longer S-R interval responses could not be determined.

To determine whether subjects might prepare a central default direction when alternative directions are more narrowly separated, we examined the distributions of force responses when targets were separated by 22° . Figure 4 shows the combined spatial distributions for the same four subjects in the unpredictable condition. For short S-R intervals, force end points are distributed broadly over a trapezoidal area formed by the correct and the wrong direction axes and vertical lines passing through the two target centers. At this interval, the distri-

¹ An overall bias towards the radial direction is evident among responses initiated in the earliest interval (≤ 80 ms). We found similar directional biases for default responses in our previous study of elbow force pulses (Favilla et al. 1989). They may reflect uncontrolled effects of prior experience or biomechanical factors

Fig. 4A, B Experiment 1. Responses by all subjects to targets with 22° separation divided into three S-R intervals. **A** Peak forces, displayed as per Fig. 3. **B** Histograms of force directions at the time of the peak dF/dt^2 , displayed as per Fig. 3

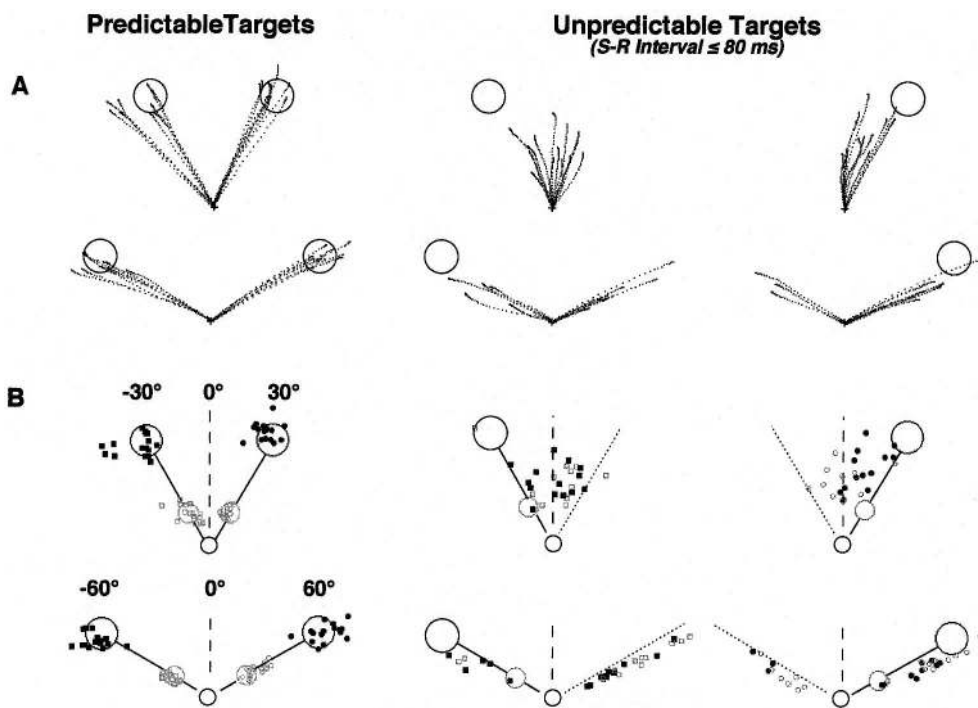
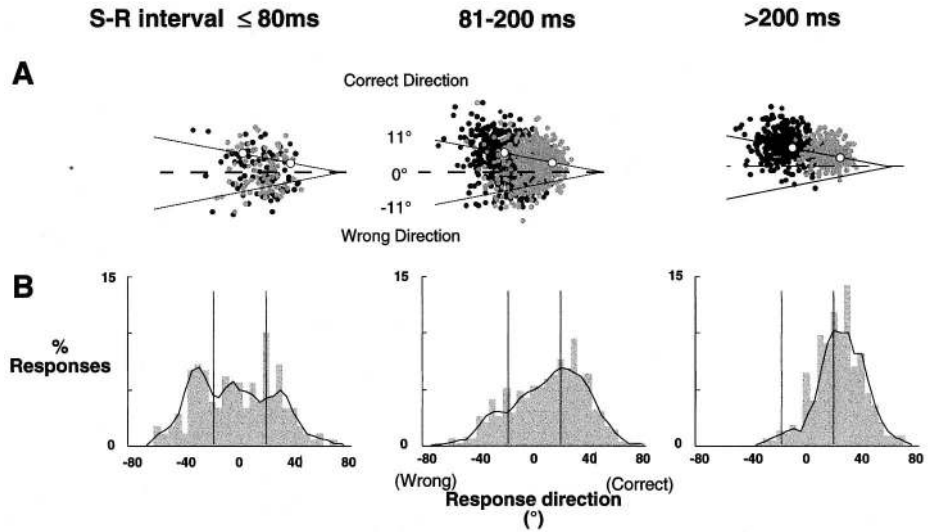
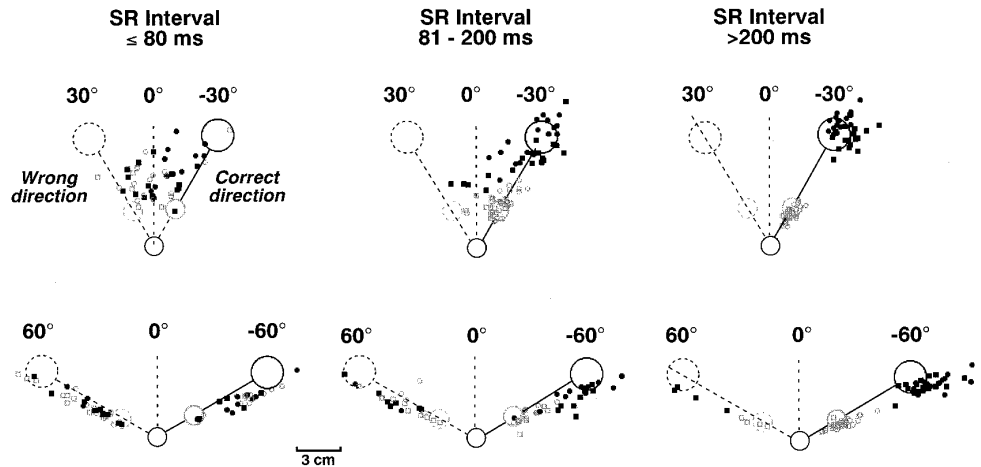


Fig. 5A, B Experiment 2. **A** Samples of hand paths to large targets separated by 60° (top) and 120° (bottom) by one subject. Hand paths shown on the left of the figure are obtained in the predictable condition for both targets. Hand paths in the center and to the right are shown for the unpredictable condition (S-R interval ≤ 80 ms) for each target separately. **B** End points of movements by the same subject to targets separated by 60° (top) and 120° (bottom). In the predictable condition (plots to the left) end points for small targets to the right are represented as open circles and to the left as open squares, for the large targets to the right as filled circles and to the left as filled squares. For the unpredictable condition (S-R intervals ≤ 80 ms: plots in the center and to the right) end points are plotted separately for movements required to reach targets to the left (open and filled squares) and to the right (open and filled circles)

tribution of initial directions (again measured at peak dF/dt) is symmetrical around zero but does not reveal conspicuous peaks. With smoothing, however, there is a suggestion of two small symmetrical peaks near the correct and wrong directions, and one in the center, at 0°. Responses to small and large force targets (gray and black circles) are intermingled in this time interval. At the second interval (81–200 ms), the directional distribution is skewed and shows a single peak centered on the correct target direction. However, the spatial distributions of force amplitudes aimed to small and large amplitude targets show some degree of separation. Finally, for intervals between 201 and 300 ms, response directions are distributed symmetrically around the correct direction, and the amplitudes of responses to the two target sizes are now substantially distinct.

Fig. 6 Experiment 2. End points of movements by one subject to targets separated by either 60° or 120° in the unpredictable condition divided into three S-R intervals. Here the end points to the left-sided targets are flipped, so that all correct direction movements are displayed as though they were to go toward the right, and all wrong direction movements are displayed as though they were to go toward the left



Thus, at both 90° and 22° subjects specify amplitude continuously and gradually from a central default value. At 90° separations, direction was specified stochastically from one or the other alternative target direction, much as we have reported for elbow forces. At the narrower separation of 22°, the directional distribution of default responses suggested the presence of both discrete and central values. However, the relatively large degree of directional variability made it difficult to determine whether at narrower target separations subjects might prepare a single central default direction, as they do for amplitude. Since a parallel series of experiments we were conducting at the time showed that directional precision was typically greater in a two-dimensional positioning task, we decided to examine this question further using that paradigm (Gordon et al. 1994b).

Experiment 2. Continuous and discrete specification of movement direction

Path characteristics and end-point distributions

When targets were precued, hand trajectories had similar features to those we have described previously for movements made without timing constraints (Gordon et al. 1994a, b). Figure 5 (left) shows these features for a representative subject: paths are straight, and end points cluster around the appropriate targets. Hand trajectories also had the expected bell-shaped velocity profiles; correspondingly, the peak tangential accelerations and velocities scaled with movement extent (not illustrated). Accuracy in these precued movements was also independent of the time of target presentation between the third and fourth tones.

With unpredictable targets (Fig. 5, right), movement accuracy was, as expected, dependent on S-R interval for both 60° and 120° separations. Although hand paths themselves remain relatively straight, end point distributions of default movements initiated at S-R intervals of 80 ms or less differed for narrow and wide target separations. At 60° separation, end points are dispersed within

a trapezoidal region with apices at the four possible target locations. End points to near and far targets, to the left and right of midline, overlap within the same region. At 120° target separation, end points are instead distributed around the two target directions. Some are aligned in the correct and some are aligned along the wrong direction. However, end points to near and far targets are intermingled within the two distributions.

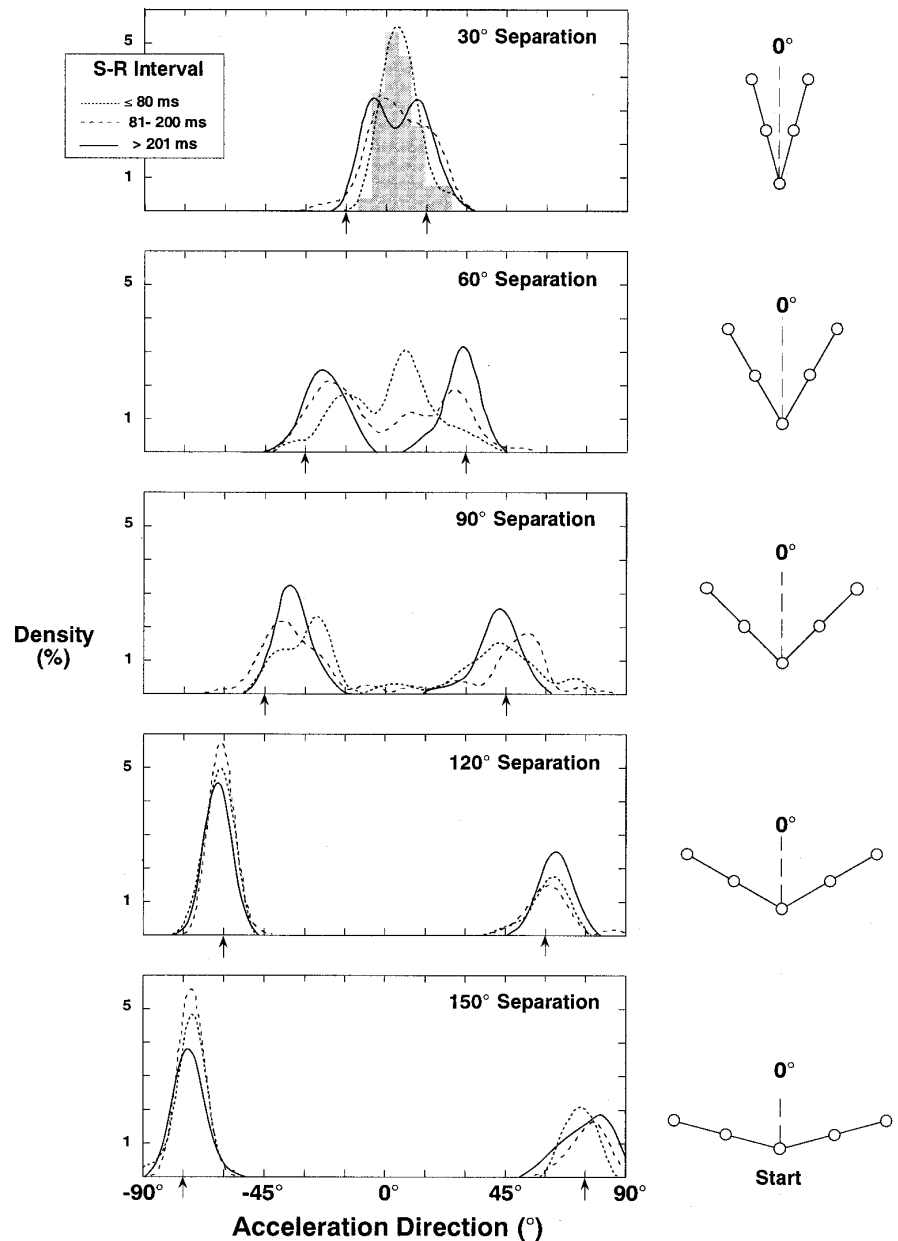
Figure 6 shows the end points of movements initiated within the same time intervals used for the force impulses in Figs. 2 and 3. Mirror-imaged data for targets to the left of midline are plotted over those to the right in order to distinguish correct and wrong direction responses. For the 60° target separation, end points migrate progressively towards their target locations in successive time bins. In contrast, for the 120° separation specification is reflected by a progressive reduction in the number of end points in the wrong direction. Thus, for narrower target separation, the default direction is in the center of the range and specification is progressive and continuous, whereas for the wider target separation the default is discrete and specification is stochastic.

The progressive improvement in extent and directional accuracy of responses to unpredictable targets took

Table 1 Means and standard errors of curvature and linearity indices across subjects ($n=5$) for predictable targets and for each time interval for unpredictable targets

	Curvature (°)		Linearity	
	Mean	SE	Mean	SE
<i>60° separation</i>				
Predictable	6.34	0.38	0.031	0.026
<80 ms	7.45	0.37	0.039	0.026
81–200 ms	8.15	0.33	0.039	0.026
>200 ms	6.58	0.35	0.031	0.025
<i>120° separation</i>				
Predictable	7.21	0.41	0.028	0.018
<80 ms	7.61	0.46	0.029	0.019
81–200 ms	8.29	0.45	0.033	0.021
>200 ms	7.33	0.39	0.030	0.019

Fig. 7 Experiment 2. Distributions of movement directions at the time of peak acceleration in one subject for five target separations. In each plot, distributions were fitted with a smooth line using a cosine function (Chambers et al. 1983). The *arrows* on the *x-axis* point to the required direction for each target separation. In the *top plot*, the actual histogram for responses with S-R intervals ≤ 80 ms is displayed to demonstrate the relationship of the fitted line to the actual distribution. On the *right side* of each plot, the actual target locations are displayed for reference



place with minimal changes in the hand paths. Table 1 shows the means and standard errors of curvature and linearity indices (see Materials and methods) across subjects ($n = 5$) for predictable targets and for each time interval for unpredictable targets. Small increases in curvature of 1° – 2° and reductions in linearity occur among movements initiated between 80 and 200 ms after target presentation. However, all values are well within the range of normal values for linearity in reaching movements (e.g. Atkeson and Hollerbach 1985; Georgopoulos 1988a, b; Georgopoulos and Massey 1988; Gordon et al. 1994b). Moreover, as can be noted among the hand paths illustrated in Fig. 5, change in direction associated with curvature did not appreciably reduce the directional error at the end point. Similarly, the improvement in accuracy was not achieved through variations in movement time.

Those data will, however, be considered in greater detail below when the systematic effects of target separation on movement time are described (see Fig. 10).

Threshold target separation for discrete directional specification

Figure 7 shows the distributions of initial movement directions in one subject at five target separations and smoothed for clarity. Data from the same three successive S-R time interval bins used in earlier figures are shown in different line types. For the 30° degree target separation, at S-R intervals ≤ 80 ms (dotted line and histogram to show effect of smoothing) initial directions are distributed unimodally around the midpoint of the range

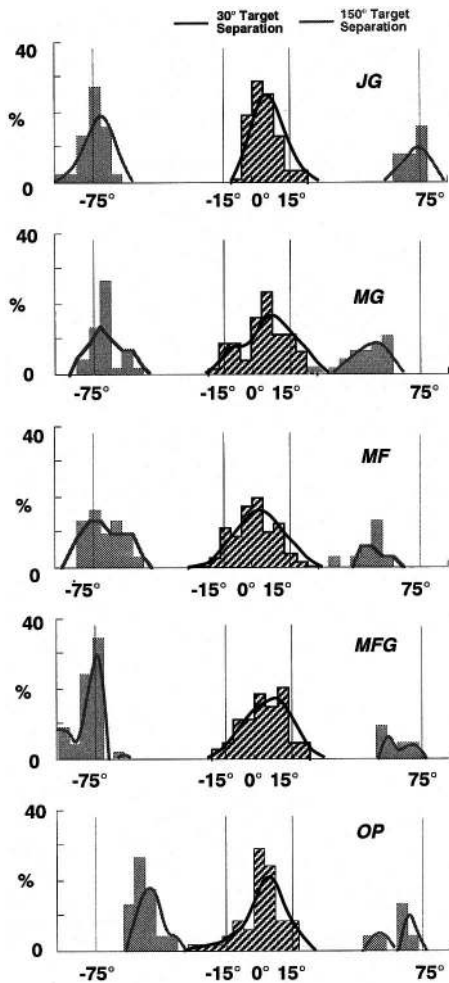


Fig. 8 Experiment 2. Histograms of movement directions at the time of peak acceleration in each subject at S-R intervals ≤ 80 ms for responses to 30° target separation (black lines) and 150° target separation (gray lines). Data are fitted with a LOWESS line as per Fig. 3. Vertical lines or arrows indicate the two sets of target directions

of possible directions. The distribution broadens and then shows two clear peaks in the two later intervals (dashed and continuous lines). By contrast, at 120° and 150° , response distributions are similar at all S-R intervals, and are centered on each target direction. The number of responses falls off symmetrically on either side so that no responses occur beyond some 17° or so of the target direction. For intermediate directional separations of 60° and 90° response distributions are bimodal but include significant numbers of responses between the alternative target directions in the early and intermediate S-R interval ranges. Thus, the threshold for discrete specification appears to be around 60° , but even at 90° a few default responses remain centered between the targets.

In all subjects direction was specified through a continuous process, beginning with a central default, for target separations of 30° , and through a discrete process and two alternative defaults for target separations of 90°

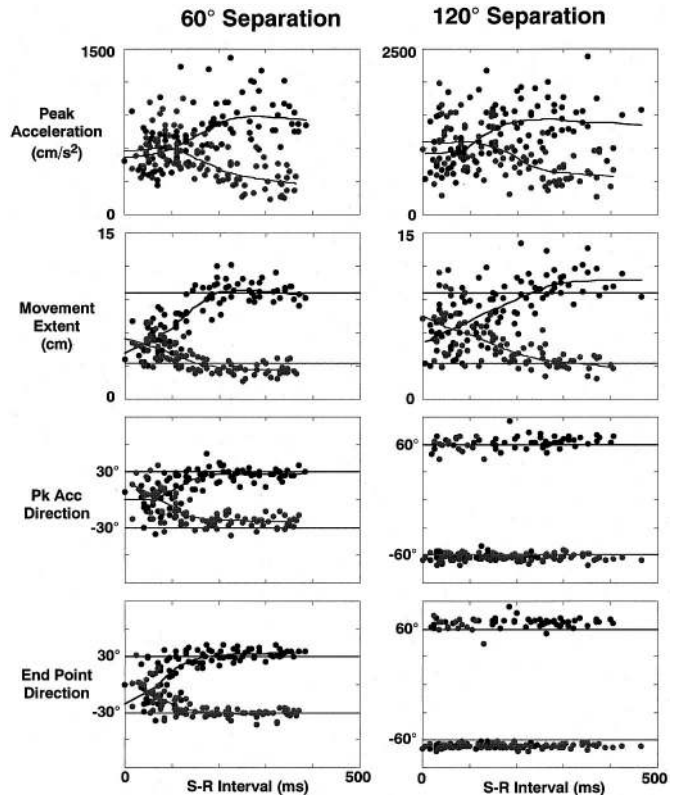


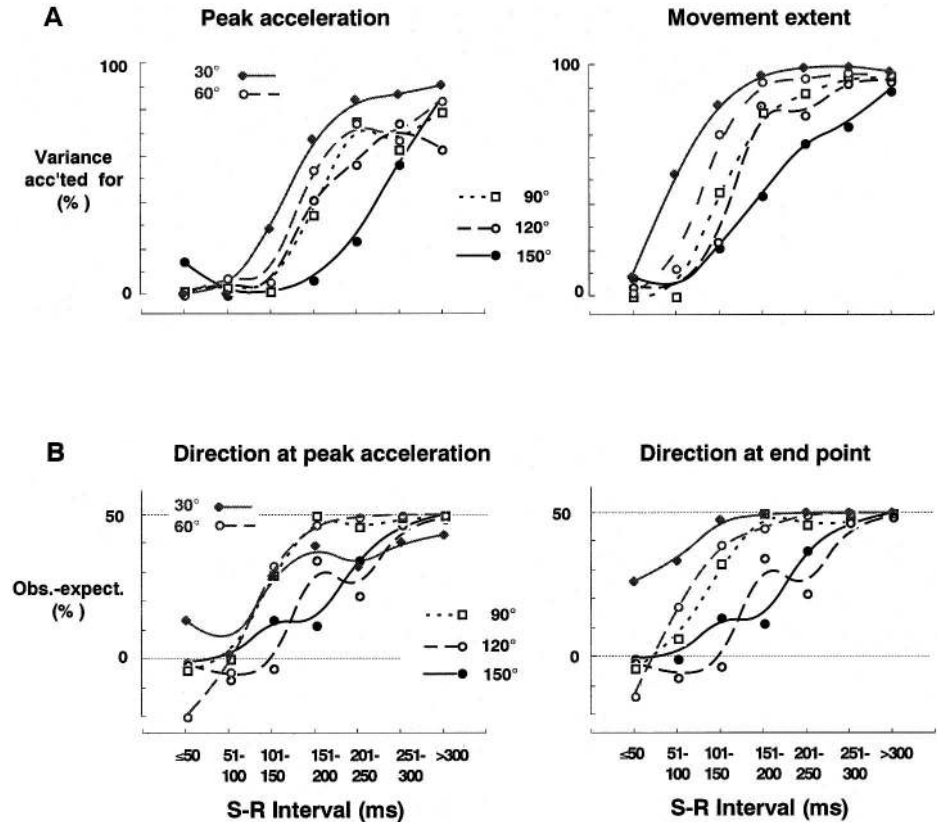
Fig. 9 Experiment 2. Peak acceleration, movement extent, direction at the time of peak acceleration, and movement direction at the end point plotted as a function of S-R interval for responses by one subject to targets with 60° separation and 120° separation. Data are fitted with LOWESS lines, while targets are indicated by continuous horizontal lines

and wider. Figure 8 shows the distributions of default response directions (i.e., S-R intervals ≤ 80 ms) for the 30° and 150° separation in all subjects. It can be seen that all subjects prepared a single intermediate direction for the 30° separation and two values for the 150° separation.

Time course of specification.

To examine the time course of specification with better resolution we next plotted the directions and extents of the movements early in the movement, at the peak acceleration, and at the end point. We used the magnitude of the peak acceleration (Gordon et al. 1994b) to estimate the extent programmed at the beginning of movement. As Fig. 9 shows for one subject, the peak accelerations and extents of individual responses gradually diverge from their central default values, both for the 60° and the 120° separations, and converge on the target values. The earlier divergence in the values of extent (~ 50 ms) than acceleration (~ 100 ms) results from the added time available for specification and updating at movement end point, when peak extent is measured (Hening et al. 1988a).

Fig. 10A, B Experiment 2. Time course of specification of peak acceleration and extent (A) and movement direction (B) in a representative subject. Data for all the movements combined were binned into successive 50-ms S-R intervals. A The squared correlation coefficient between peak acceleration and target extent, as well as between movement extent and target extent, were computed and plotted separately for the five target separations. In B The differences between the percentages of observed and expected responses in the correct direction at the time of peak acceleration and at the end point were plotted for the five target separations separately



Directional specification also takes the form of a gradual shift in initial direction for the 60° separation. However, at the 120° separation both initial and final directions remain grouped around the directions of the two targets throughout the specification interval. The two modes of specification can be seen to be associated with differences in variability. For short S-R intervals, variability in extent and in peak acceleration are quite large initially and decrease progressively in the course of specification. The same is true for directional variability at 60° separation. At 120°, however, both correct and wrong direction responses are already tightly grouped around the target values even at short S-R intervals. Thus, the continuous mode of default selection and specification is associated with a progressive reduction in variability, whereas the discrete mode is not: direction is specified with as high a precision in defaults as it is in fully specified movements. A final point to note in Fig. 9 is that acceleration and extent begin to be specified substantially earlier for narrow than for wide directional separations, suggesting an interaction between extent and direction specification.

To quantify the degree of specification and to compare the rate of specification for different directional separations we computed the amount of variance in response measures accounted for by variance in the target in successive 50-ms S-R interval time bins (Hening et al. 1988a). Figure 10A shows the squared correlation coefficients (r^2) of peak acceleration (left) and extent (right) to target distance for each of the five target separations. Al-

though response variance accounted for by the target always increases progressively, specification occurs earlier for the narrower target separations. The same phenomenon was evident in all subjects. To document this across subjects we compared the time at which target distance accounted for 50% of the peak acceleration and distance variance at the two extremes of directional separation. For the 30° separation this was achieved by the 151–200 ms S-R interval. For the 150° separation it occurred 100 ms later (in the 251–300 ms interval). Corresponding values for extent were 51–100 ms and 151–200 ms.

Because for some separations direction was specified discretely and the linear correlation requires a continuous range of values for one variable at least, we could not use the same index to assess the time course of directional specification. We computed instead the percentage of observed responses in the correct direction at peak acceleration and at end point in each 50-ms time interval. We then performed a chi-square analysis to assess the significance of the difference between observed and expected correct responses. To avoid effects caused by differences in the rate of specification of correct and wrong direction responses, we separated responses in the hemispaces on one side or the other of the line bisecting the angle formed by the pairs of targets. Figure 10 shows that, like extent, direction is specified progressively and that this occurs earlier for narrow than for wide target separations. As before, the earlier specification of direction at the end point than at peak acceleration reflects an updating process (Hening et al. 1988a).

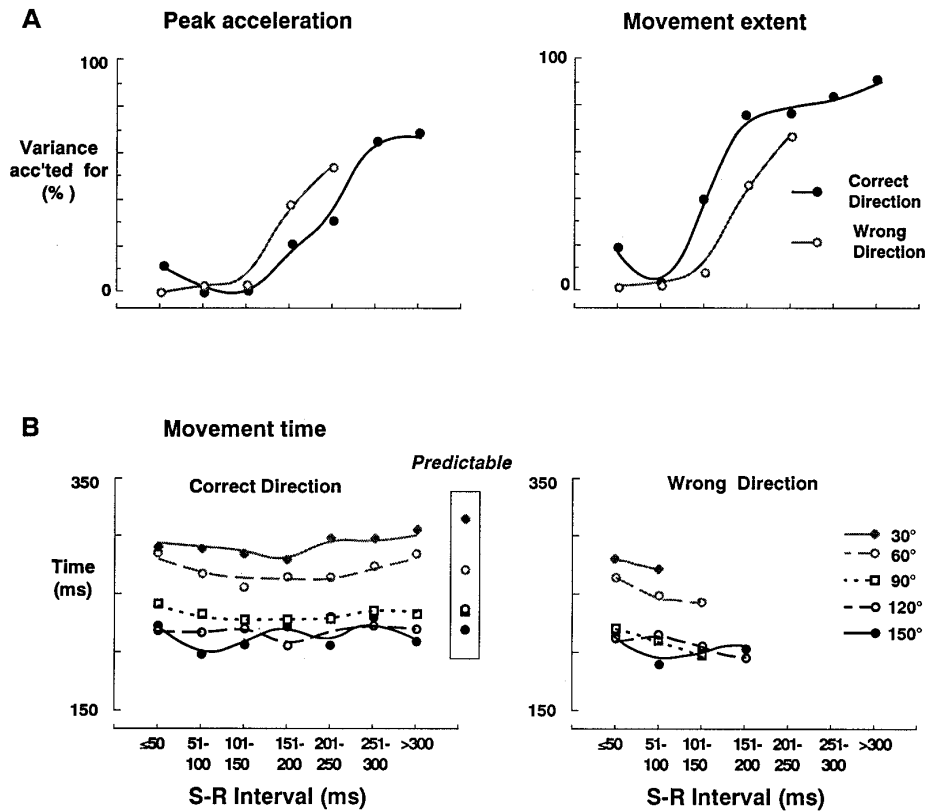


Fig. 11A, B Experiment 2. **A** Time course of specification of peak acceleration and extent in a representative subject. Data for 120° and 150° were combined and binned into successive 50-ms S-R intervals. Squared correlation coefficients between peak acceleration and extent and target extent were plotted separately for movements with correct and wrong direction. For peak acceleration, r values were statistically significant ($P < 0.05$) only for responses in the correct direction for S-R interval ≥ 151 ms. For responses in the wrong direction no r value reached statistical significance due to the small samples. For movement extent, r values were statistically significant for S-R interval ≥ 101 ms for responses in the correct direction and for S-R interval ≥ 151 ms for responses in the wrong direction. **B** Mean movement times for movements binned into successive 50-ms S-R intervals to all five target separations. The plot to the *right* displays the results for movements in the correct direction only, while the plot to the *left* is for movements in the wrong direction. The points on the *inset* show the mean movement time for the predictable condition

Extent specification in wrong direction movements

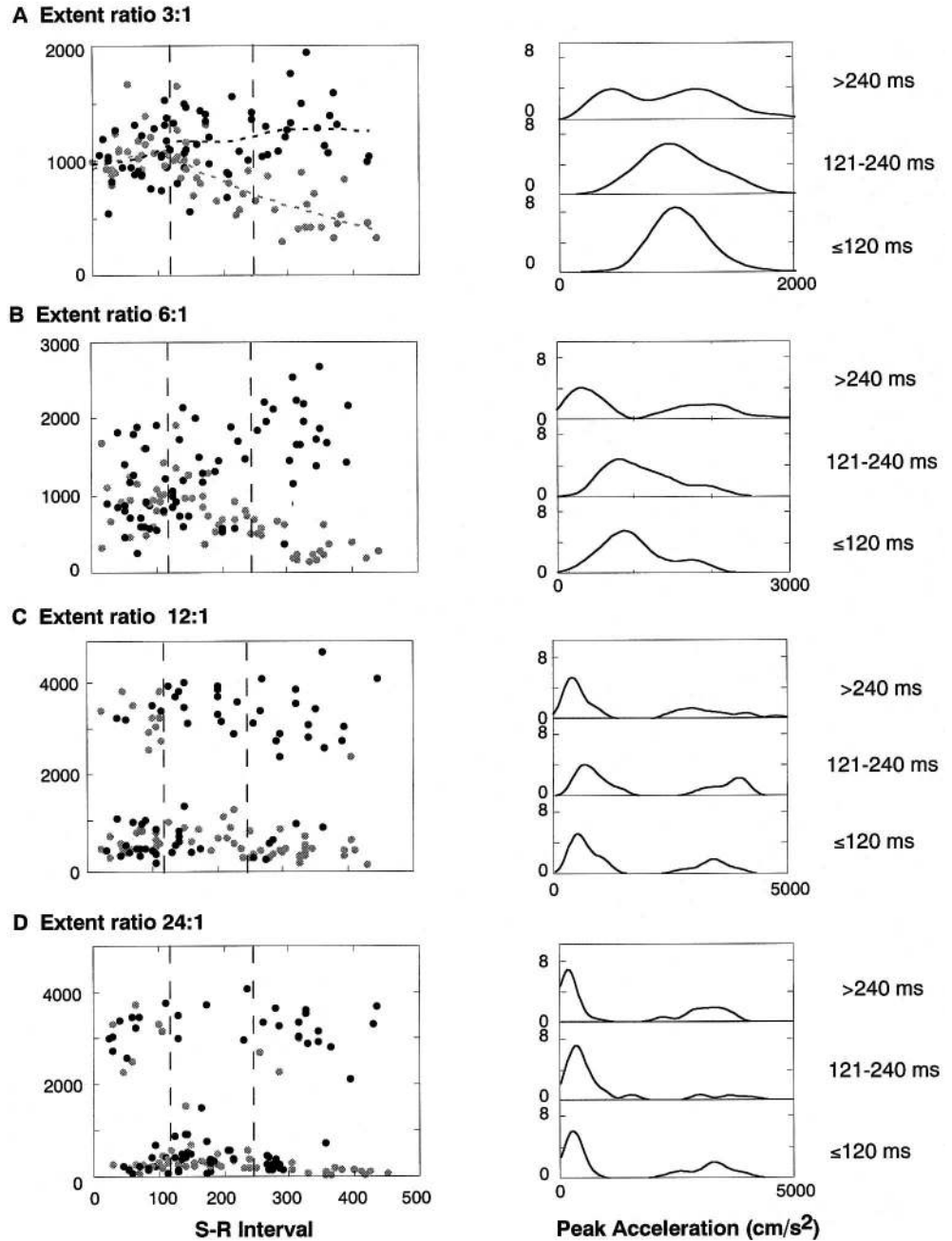
Since responses can only be assigned unambiguously to correct and incorrect directions at the 120° and 150° target separations, we focused on these to determine whether extent was specified independently of direction. To increase the number of movements in each time bin we combined responses made with both target separations since the rate of specification (Fig. 10) and movement times (see below) were not different. Figure 11A shows that peak accelerations and final extents of correct and incorrect direction movements are both specified progressively. Thus, as we reported for amplitude and direction of elbow force pulses, the extent of hand movements

may be specified independently of direction. However, as noted in that case as well, the rate of extent specification, measured in this way, was lower for responses in the wrong direction though less so for acceleration.

The increase in acceleration variance accounted for by target distance across S-R intervals indicates that the improved accuracy resulted primarily from progressive improvement in the linear scaling of trajectories to the target. However, it was also possible that subjects altered their strategy when targets were unpredictable and prolonged movements to distant targets to a greater degree than for predictable targets. To examine this, we first determined the effect of processing time on mean movement duration. Although Fig. 11B shows that mean movement times varied for the different target separations, among responses in the correct hemisphere they did not vary with S-R interval (left). Since movement times were similar for predictable targets (boxed symbols in Fig. 11B) the dependence on target separation is not attributable to the processing of target information. Moreover, the slope of the relationship of movement extent to peak acceleration was also invariant across S-R intervals (not illustrated). Thus, subjects did not revert to a "width control" strategy to improve the accuracy of their movements when insufficient information about the target location was available to them. On the other hand, the data in Fig. 11 (right) show that duration is progressively reduced among wrong direction responses. Interestingly, this occurs both for narrow and for wide target separations and suggests that subjects tended to abort response if their direction was incorrect.

Fig. 12A–D Experiment 3.

Time course of specification of peak acceleration for targets at different distances but with the same direction in a representative subject. In the *left column*, peak accelerations are plotted as function of S-R interval for four target separations. *Black dots* are for responses requiring higher peak acceleration (i.e., they should have been directed to the large distance targets) and *gray dots* are for responses requiring lower peak acceleration (i.e., they should have been directed to the small distance targets). The *vertical dashed lines* at 120 and 240 ms indicate the three S-R intervals (≤ 120 ms, 121–240 ms, and > 240 ms) selected to plot the corresponding distribution of peak accelerations in the right column. In each plot, distributions were fitted with a smooth line using a cosine function, as per Fig. 6



The striking dependence of movement time on target separation is likely to be due to differences in the mean inertial and gravitational loading of hand movements in the different pairs of directions. Movements directed to the targets at $\pm 15^\circ$ from the straight-ahead direction (i.e. the 30° separation) required both elbow extension and shoulder flexion. As target separation increased, shoulder flexion was increasingly replaced by external rotation for movements to the right and by internal rotation for movements to the left. As noted in the prior studies with the same arm configuration (Gordon et al. 1994a), this reduces inertial and gravitational resistance, hand acceleration becomes higher and movement time becomes shorter to compensate for this.

The same effects were seen in all other subjects; thus a multifactorial ANOVA showed a significant effect of target separation ($P < 0.0001$) but no effect of S-R interval ($P = 0.96$) on movement time. In sum, these data indicate that specification entails a gradual rescaling of the overall response to the particular target rather than significant modulation of movement time.

Experiment 3. Discrete specification of extent with large distance separations

To explore whether movement extent may be specified discretely when differences in target distance are large,

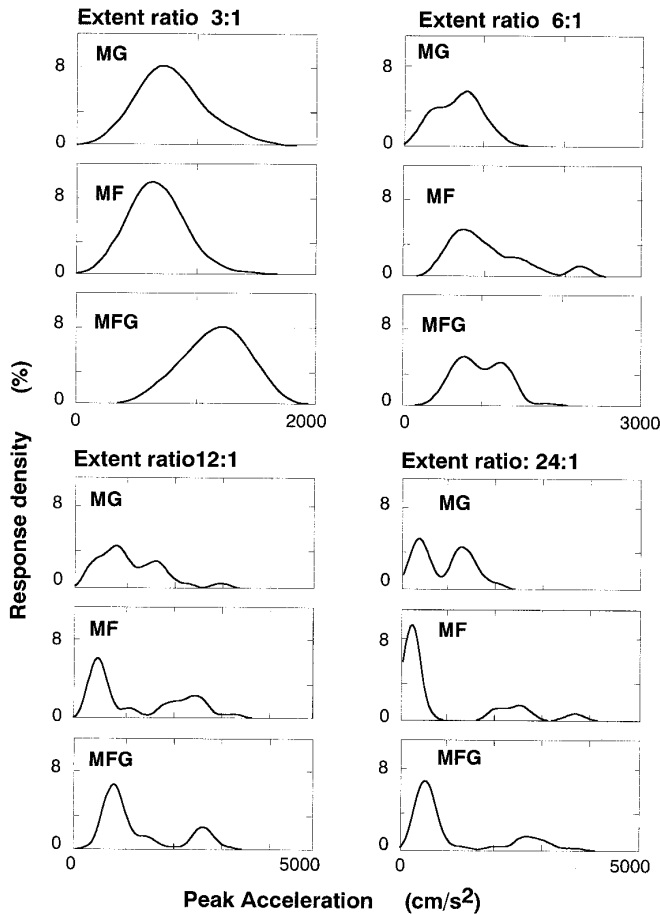


Fig. 13 Experiment 3. Distribution of peak accelerations for four target separations in three subjects at the earliest S-R interval (≤ 120 ms). Distributions were fitted with a smooth line using a cosine function, as per Fig. 6

we examined the time course of specification for different target separations. As noted in Materials and methods, four subjects were tested in the timed response paradigm, using two targets at different distances but in the same direction from the starting position. Since the total movement extent reflects both pre-programmed specification and later corrections, we analyzed differences in specification from peak accelerations, which represent an estimate of the initial programmed extent.

As shown in Fig. 12 for one subject, peak accelerations of movements initiated at S-R interval ≤ 120 ms are clustered in a single group for the smallest distance ratios. Peak accelerations then diverge progressively to form two separate groups of responses. By contrast, for both the 12:1 and the 24:1 ratios, two separate clusters of values for the peak accelerations are evident even in the earliest time intervals. These include responses to both the near and far targets. With increasing processing time, specification takes the form of a progressive reduction in the number of misprogrammed accelerations.

The other three subjects also show default responses with unimodally distributed peak accelerations for the smallest distance ratio and bimodal distributions for the

largest (Fig. 13). For intermediate ratios some differences are apparent: MFG and MF show two distinct peaks, whereas MG shows a relatively broad distribution.

Discussion

The three experiments reported here sought to characterize the time course with which wrist forces and planar hand movements are specified by visuo-spatial information. We specifically wished to determine how subject expectation and distances concerning the range of possible target directions and motor set – and the nature of the processing taking place once target location was displayed. Our findings confirm the basic conclusions concerning the partitioning of these processes derived from our earlier studies of elbow force pulses. When expecting to direct forces or hand movements to a target, subjects prepare a specific response, presumably by loading its representation in a working memory response buffer for later release. When the target is predictable, as here, by being precued or, as in previous studies, by being embedded in a predictable sequence, this default response is accurate and is not substantially influenced by further information. When the upcoming target is unpredictable, the prepared or default response, while adapted to the range of expected targets, does not begin to be matched to the specific target presented until some 100 ms or more. Extent and direction are then specified progressively over a period of 200 ms or more. Other trajectory features, notably movement time and linearity, remain essentially unchanged. The extended time course of specification represents a significant limitation that the nervous system must overcome in producing accurate movements when urgent responding is necessary.

In the remarks that follow we discuss first certain implications of the finding that specification takes the form of a continuous process for small disparities in expected directions or distances and a discrete stochastic process when these parameters differ substantially. We then consider the significance of these observations for the representation and planning of hand trajectories to visual targets and for the respective roles of preparatory and visuo-motor mechanisms in these processes.

Continuous and discrete modes of specification

A prominent aspect of the results shown here was that subjects prepared default responses in one or the other direction even though, biomechanically, this variable could assume intermediate values. Specification was stochastic and manifest as a progressive increase in the proportion of responses in the correct direction rather than as a gradual change in direction of all responses. Thus, for separations of 120° or more, directional variability around the two alternate target directions did not change appreciably over time. On the other hand, for directional

separations of 60° or less there were increasing numbers of responses directed between the two alternative directions, and at 30° default responses were distributed exclusively around this central direction. Specification then evolved continuously, as a progressive change of the mean towards the target direction together with a progressive reduction in directional variability. The results of experiment 3 suggest that the specification of movement extent follows the same principle, namely continuous specification from a central or average default for narrow separations and discrete specification for wide separations.

Two distinct modes of preparation and specification have also been observed for ocular saccades by Ottes and co-workers (1984). Those authors reported a similar critical dependence of saccade direction on the angular separation of potential visual targets: saccades initiated at short latency to two simultaneous visual targets are often directed towards a position intermediate between the targets if target separation is narrow, a behavior referred to as “averaging”, but to one or the other if targets are widely separated. Recent experiments by Sparks and colleagues using the timed response paradigm indicate that the “averaging” in short-latency saccades reflects incomplete specification (Stanford et al. 1990) much as has been documented for limb movements in reaction time paradigms (Favilla et al. 1987; van Sonderen et al. 1988).

Continuous specification and mental rotation

The phenomenon of “mental rotation” studied by Georgopoulos and co-workers (Georgopoulos and Massey 1987; Georgopoulos 1990) suggests a possible neural mechanism underlying the gradual shift in direction that occurs with narrowly separated directions. Those authors showed systematic increases in reaction time when subjects were required to deviate the direction of intended movements to visual targets. Interestingly, reaction time increased linearly with the magnitude of the instructed rotation of the movement, as though the specified direction rotated through intermediate directions at a constant rate. It was therefore significant that this linear dependence was associated with a progressive rotation in the direction of population vectors derived from task-related activity of motor cortex neurons: the “intended” direction swept progressively across intermediate directions. It seems plausible that the same would take place during specification, as movements directions shift from a central default towards the actual target. This same group has also recently provided interesting results indicating that the motor cortex is recruited in a different way when response directions are predetermined as discrete values (Pellizzer et al. 1995). Thus, when monkeys execute a sequence of movements in different directions, motor cortical population vectors shift abruptly from one direction to another without passing through intermediate values.

The progressive rotation of a population vector could account for the increase in time needed to specify direction with increasing deviation of the required from the

default direction. However, it is less clear why directional separation should systematically delay and prolong extent specification as noted here and by others in a precuing task (Bock and Arnold 1992). In our previous study of elbow force pulses we speculated that prolongation of extent specification by a concurrent demand for specifying direction might reflect a common attentional or timing resource for both processes (Sperling and Dosher 1987; Brown and Marsden 1991).

Discrete specification in sensory processing

An interesting parallel exists between the discrete specification of response parameters reported here for large disparities of distance and direction and the phenomenon of categorical perception of sensory stimuli (for review see Harnad 1987). This term, which was coined originally by Liberman and co-workers (Liberman et al. 1957, 1961) for speech sounds, describes observations that stimuli varying along a physical continuum may be identified with discrete perceptual responses or categories. Categorical boundaries are typically not fixed but vary with task context or with subjects’ prior experience (Repp and Liberman 1987). The narrower directional separation of target required for discrete specification of wrist force direction versus whole arm movement direction may represent such a context dependency. However, further experiments would be needed to define the origin of this dependency. Categorical perception differs from other forms of psychological categorization in that the discriminability of equally spaced stimuli is greater across category boundaries (i.e., from one category to another) than within categories (Pastore 1987). The reduced variability of discrete default directions, evident for example in Fig. 9, could represent an analogous phenomenon. Further experiments would be necessary to determine what common features may underlie the sharpening of boundaries in cognitive and motor representations.

Extent and direction in the planning of two-degree-of-freedom movements

Since the observations of Morasso (Morasso 1981; Abend et al. 1982) it has been widely believed that hand movements to visual targets are planned in extrinsic spatial coordinates, without taking account of the complexity inherent in controlling individual joint motions (cf., however, Hollerbach et al. 1987). Recent studies of the sources of errors in movements to visual targets suggest that hand movement planning may be further simplified by converting target location to a vector through which the nervous system specifies extent and direction (Bock and Eckmiller 1986; Bock et al. 1990; Ghez et al. 1990; Bock 1992). For example, the finding that extent variability shows a pronounced dependence on target distance while directional variability does not, suggests that extent and direction are planned independently (Ghez et

al. 1990; Gordon et al. 1994b). In accord with a vectorial plan, we and others have reported that directional accuracy requires explicit visual information about initial hand position (Ghilardi et al. 1991, 1995; Ghez et al. 1993, 1994; Rossetti et al. 1994). When visual information is unavailable systematic directional biases occur that appear to reflect biased estimates of the initial hand position in the workspace relative to the egocentric axis (Ghilardi et al. 1995).

The results reported here provide further support for such vectorial planning in two ways. First, the finding that extent and direction are specified in parallel over time is the temporal complement of the independent spatial variability in these parameters reported earlier (Gordon et al. 1994b). Second, the finding that mean movement time remains unchanged across the specification interval indicates that variations in movement duration are fully determined by variations in target distance. Thus, no additional process needs to specify movement time.

The determinate and scalable time course of hand trajectories is consistent with the idea that individual movements are represented by the brain as individual units, which may be considered as spatio-temporal "primitives". This conforms with the idea proposed for more complex movements by Lacquaniti and coworkers (Lacquaniti 1989). Indeed, the drawing of specific shapes or scribbles comprises discrete isochronous segments (Viviani and McCollum 1983) during which the rate of angular deviation remains relatively constant (Lacquaniti et al. 1983). Thus, for point-to-point hand movements, subjects select a given tempo and a near-zero rate of angular deviation as defaults. Recent observations by Maitra and Cooke (1996) indicate that the nature of the aiming task determines the degree of hand path linearity.

The present findings of systematic differences in movement time according to target separation suggest that differences in effector dynamics are, at least to some extent, taken into account in the selection of the response primitive. Whether this requires a secondary representation of movement in intrinsic coordinates as suggested by Lacquaniti (1989), or whether the transformation from vectorial coordinates arises from some other mechanism, is a subject for future studies.

The objection could be raised that the consistency of movement time and the linearity of hand paths across S-R intervals could have reflected the instruction given to subjects not to correct their movements. We do not, however, feel this is likely since the number of submovements that subjects generate appears to be essentially adaptive and preplanned (Meyer et al. 1982, 1990; Worringham and Stelmach 1990). In general, the number of submovements tends to decrease with practice as subjects cover increasing proportions of the target distance in the initial submovement (Brooks et al. 1996). Similarly, subjects adjust hand path curvature adaptively over successive trials in visually distorted virtual environments (Wolpert et al. 1995).

The ability of subjects to dissociate initiation from specification for both extent and direction indicates that the two are governed by distinct neural processes operating in parallel. We hypothesize that in the timed response task, initiation is triggered by a timing element (Wing et

al. 1984; Leak and Gibbon 1995) acting on a response buffer in working memory. This buffer contains the representation of the next motor response, perhaps as a response, primitive, to provide a temporal profile of excitation to segmental neural networks. This specifies a unique spatial path and velocity profile.

In addition, we hypothesize that preparatory processing also determines a visuo-motor transform consisting of a vectorial map of a restricted region of visual space where task-related behavior is defined (Ghez et al. 1983; Martin and Ghez 1985). Such a transform implies a learned scaling or gain (Bock 1992; Pine et al. 1996) and reference axes to represent the origin of the vector (Ghilardi et al. 1995). The neural implementation of this task-related mapping may be mediated by parietal association cortex, plausibly through context-dependent gating and biasing of sensory inputs (Mountcastle et al. 1975; Kalaska 1988).

A distinctive feature of our model of trajectory specification is that most decisions can be made "off-line" during the preparatory period rather than in the interval between stimulus and response. Once the response primitive is loaded into the working memory buffer and the visuo-motor transformation is in place, the response is fully determined by the spatial location of the target, the rate at which extent and direction are updated and the time of movement initiation. This mapping allows stimuli present anywhere in the workspace defined by the task to be functionally equivalent and obviates delays introduced by choice effects. In point-to-point movements, the scaling factor linking visual coordinates to the hand movement vectors varies in different tasks and must be acquired through learning. Additionally, variations in initial hand position may require new reference axes, which also have to be learned (Ghilardi et al. 1995). The stimulus-response maps allow choice effects on response latency to decrease and disappear with practice (e.g., Mowbray and Rhoades 1959; Ghez and Vicario 1978a; Georgopoulos et al. 1981; Hening et al. 1988b). The benefit of shifting decisions "off-line" to the preparatory interval is that multiple decisions may be made in parallel without interfering with the actual response. The complex operations implicit in preparatory events are consistent with the long 1–1.5 s time course of premotor potentials that precede self-initiated voluntary movements (Kornhuber and Deecke 1965; Deecke and Kornhuber 1976; MacKay and Bonnet 1990). Such potentials are also present in reaction time tasks and thus precede the occurrence of randomly presented stimuli. However, this only occurs if interstimulus intervals are not much more than 3 s (Jahanshani et al. 1995). This may reflect the inherent risk of remaining in a fully prepared and determinate state, should an unexpected event demanding action arise.

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