Research Report

THE ROLE OF INHIBITION IN THE REGULATION OF SEQUENTIAL ACTION

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Abstract—*We investigated the regulation of sequential action using a new paradigm. Participants learned a sequence of seven stimulus categories and then monitored for them during successive displays. All displays were instances of these categories, presented in pseudorandom order. On each trial, participants monitored for an instance of Category 1, pressed a key on a computer keyboard, then monitored for an instance of Category 2, pressed a key on the keyboard, and so on for all seven categories. Thus, a perfect trial contained exactly seven responses. Intrusion errors were classified as a function of ordinal distance from the current serial position (*n*). Fewer intrusion errors were made at near serial positions than at far ones, suggesting a gradient of lateral inhibition. In addition, more intrusions were made on* n + 1 *categories than* n − 1 *categories, suggesting greater availability of intended than completed goals. In accord with current models of sequential action, the results indicate lateral and self-inhibition as important mechanisms in regulation of sequential action.*

Everyday behavior often consists of action sequences, rather than actions in isolation (Miller, Galanter, & Pribram, 1960). Consider the task of changing lanes while driving. This entails a fixed series of actions that should be carried out in a fixed order (e.g., activating the signal light before moving to the next lane) and only when the environmental conditions indicate that the next action can take place (e.g., wait for a sufficient gap in traffic before changing lanes).

Although everyday action sequences are routinized, action slips (omitting an intended action), perseverations (repeating previously completed actions), and anticipation errors (carrying out an action too early in the sequence) can be observed in both everyday and laboratory tasks (e.g., Della Malva, Stuss, D'Alton, & Willmer, 1993; Duncan, Emslie, Williams, Johnson, & Freer, 1996; Humphreys & Forde, 1998; Norman, 1981; Reason, 1984). This implies that although the order of actions may be perfectly memorized, there are underlying mechanisms that serve to propel the action sequence forward, and that may be affected by distraction or lapses of attention. In the driving example, a salient gap in traffic might lure the driver into changing lanes before signaling properly. In the present study, we attempted to capture these features of sequential behavior in a laboratory task.

SEQUENTIAL BEHAVIOR

It has long been assumed that the generation of sequential actions requires the parallel activation of all actions belonging to the sequence before their execution (Estes, 1972; Lashley, 1951). By this view, all actions within a given sequence, and not just the currently relevant one, are highly active during sequential behavior. Consequently, there is a need for additional mechanisms of selection to ensure that a given action is carried out in correct serial order.

On the basis of these assumptions, neural network models of sequential-action regulation often feature a winner-take-all architecture, in which the currently relevant node, or action, inhibits all competing nodes (lateral inhibition: cf. Glasspool & Houghton, 1998; Houghton, 1990; Houghton & Tipper, 1996; see Shallice, 1972, for similar ideas). In some models, such as the Competitive Queuing model proposed by Houghton (1990), this feature is coupled with the concept of self-inhibition, in which a just-completed action undergoes inhibition to make the next action the most highly activated and thus propel the sequence forward. Self-inhibition results in an asymmetry in the availability of those actions already performed and those yet to be performed. Similar mechanisms have been incorporated in models of language production (e.g., Dell, Burger, & Svec, 1997; MacKay, 1987), spelling (e.g., Houghton, Glasspool, & Shallice, 1994), and task-set switching (Mayr & Keele, 2000). For example, Dell et al. (1997) demonstrated that this asymmetry results in a greater proportion of anticipatory (e.g., "cu*ff* of coffee") than perseveratory ("cup of co*p*y") errors in practiced speech. Similarly, recent models of verbal short-term serial recall posit that a self-inhibition mechanism is applied to generated items (e.g., Brown & Vousden, 1998; Burgess & Hitch, 1992, 1999; Henson, 1998; Page & Norris, 1998; Vousden & Brown, 1998). Because self-inhibition decays over time, suppression is considered greater for ordinally near items (lag −1) compared with distant items (lag −2 and earlier).

The regulation of sequential action is also of relevance to the study of prospective memory, or memory for intended actions, broadly defined. Recent findings indicate that intended actions have a higher activation status than neutral action schemas (the intention superiority effect: Goschke & Kuhl, 1993). In addition, Marsh and colleagues further demonstrated that just-completed and canceled action plans undergo suppression compared with neutral action plans (Marsh, Hicks, & Bink, 1998; Marsh, Hicks, & Bryan, 1999). For example, Marsh et al. (1999) gave participants two action plans composed of multiple, unrelated actions. One was designated the plan to be completed (relevant) and the other was irrelevant. In a lexical decision task, words associated with the relevant plan were more quickly identified than those associated with the irrelevant plan. Following the completion of the action plan, the opposite was true, which Marsh et al. interpreted as evidence for the suppression of completed actions. These findings are consistent with the idea of self-inhibition in the more general case of sequential-action regulation. To our knowledge, however, the intention superiority effect and suppression of completed actions have not yet been examined within a fixed series of intended actions.

OBJECTIVES AND RESEARCH STRATEGY

Our general aim is to study the mechanisms involved in the regulation of sequential action. Specifically, we sought in this study to

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develop a task that allows for measuring the relative availability of competing goals and observing lateral and self-inhibition processes. We operationalized the action sequence as a series of goals, or stimulus categories. Participants learned the goal sequence, and were instructed to monitor consecutively presented stimulus displays and press a key on a computer keyboard when they first saw an instance of Goal 1. They then monitored the displays for instances of Goal 2 and made a response, and so on, until all seven goals were executed in a trial.

In relation to previous work, the design added several features: First, participants were required to carry out seven goals, the order of which was always visible so that we could more clearly measure the regulation and updating of sequential action without confounding memory for serial order. Second, participants were trained extensively on the sequential-action task to ensure that the sequence was overlearned. Third, we aimed to simulate the effect of distraction by presenting foils in between target items that were instances of the competing goals. By examining the intrusion errors in response to foil items, we could assess the availability of competing goals at different points in the sequence.

On the basis of previous models of sequential action, we expected that intrusion errors would be less prevalent for recently completed goals and goals in the near future than for more distant goals, indicating a gradient of lateral inhibition. Further, we expected that self-inhibition would result in an asymmetry of intrusion errors, with more intrusions made for intended goals than for completed goals.

METHOD

Participants

Thirty-two young adults, 20 to 30 years of age, were recruited from the Free University, Berlin, and Humboldt-University, Berlin, and were paid 20 German Marks per hour. All participants signed a written consent form prior to testing.

Materials

Exemplars of the seven goal categories (numerals, letters, geometric figures, math symbols, Chinese characters, pipe symbols, and freehand figures) are shown in Figure 1. In each stimulus frame, the exemplars were shown within a white square (approximately 4 × 4 cm) on a dark gray background. Stimuli were always presented in pairs, randomly drawn from nine possible exemplars within a category. Across participants, the goal categories were assigned equally often to each ordinal position (Goals 1–7), so that any two goal categories would not occur successively in more than two counterbalancing orders.

During each unscored practice trial, participants were prompted with a visual indicator of the currently relevant goal. During all test trials, a cue card depicting the sequence order was visible, but participants did not receive any indication of their current serial position. If an error was made, a feedback screen interrupted the trial and indicated the next goal.

Design and Procedure

Within each session, participants worked on two to seven blocks of 49 trials. Trial length ranged from 11 to 17 stimulus frames. Stimulus order was predetermined so that there were equal numbers of opportunities to make anticipation and perseveration errors, and so that equal numbers of target and nontarget items were shown.

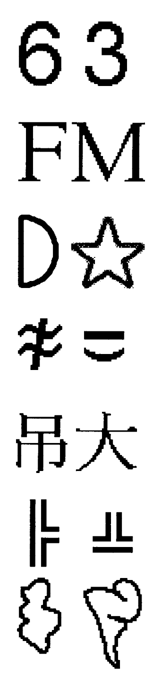

Fig. 1. Example of a participant's fixed goal sequence.

The experiment spanned seven 1-hr sessions. In Session 1, participants were trained to recognize the exemplars from each category by monitoring and key-pressing for one category per block. The order of categories was the same as the goal sequence used in the following multiple-goal conditions. In Session 2, participants were taught their goal sequence, then performed one practice block and two test blocks with a stimulus duration of 150 ms and an interstimulus interval (ISI) of 1,000 ms. In Sessions 3 through 5 (three blocks per session), the ISI on each trial was decreased 5% of the previous trial's ISI if performance was perfect, and increased 5% if at least one error was made on the previous trial. In Sessions 6 and 7, participants returned to the 1,000-ms ISI for two blocks per session so we could compare performance before and after adaptive training. Figure 2 shows a trial sequence.

RESULTS

To measure the relative availability (e.g., net activation) of competing goals, we classified intrusion errors in terms of their ordinal distance from the current goal. For example, if a participant were monitoring for an instance of Goal 3, but in the meantime responded incorrectly to an instance of Goal 1, that would be considered a lag −2 error. We classified all intrusion errors according to the following categories: lag ≤−4, lag −3, lag −2, lag −1, lag +1, lag +2, lag +3, lag ≥+4. Error rates were calculated on the basis of the number of opportunities to commit intrusions within each lag type.

Repeated measures multivariate analyses of variance with the lag

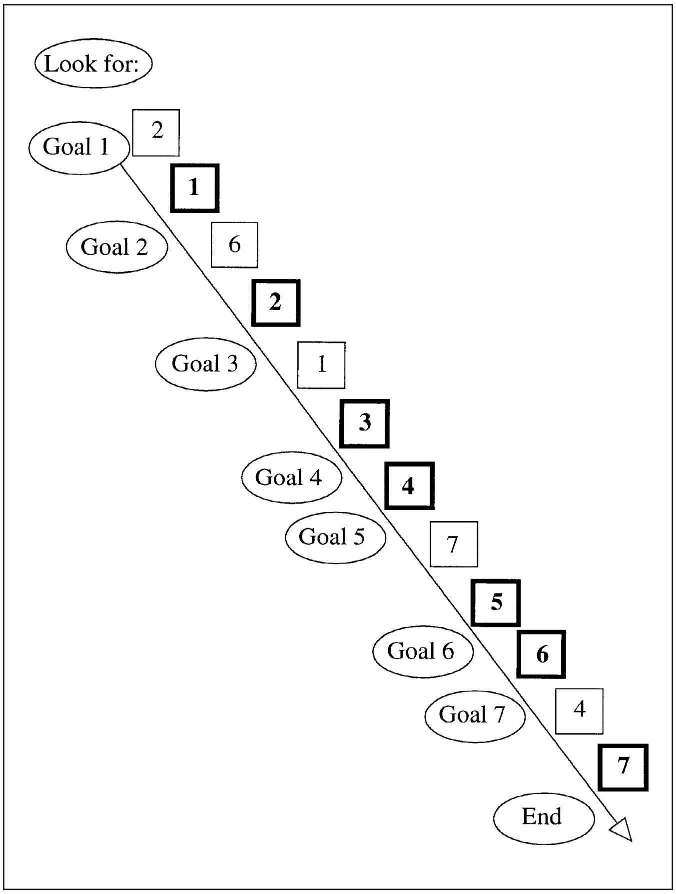

Fig. 2. Example trial from the sequential-action task. Numerals in the boxes refer to the serial positions of the goals and are not actual stimuli. Boxes in boldface indicate target stimuli in response to which participants were to press a key on a computer keyboard. Goal numbers in the ovals indicate the currently relevant goal to be detected.

factor ($\leq -4, -3, -2, -1, +1, +2, +3, \geq +4$) were carried out separately for the three phases of the experiment: fixed ISI before adaptive training (Phase 1), adaptive training (Phase 2), and fixed ISI after adaptive training (Phase 3). Figure 3 depicts the mean intrusion error rates by lag and phase. In Phase 1, the lag effect was nonsignificant, $F(7, 25) = 1.92$, $p = .11$, $MSE = 0.003$, possibly owing to variability in accuracy at the beginning of training. However, lag effects were significant for Phase 2, $F(7, 25) = 4.50$, $p = .002$, $MSE = 0.002$, and Phase 3, $F(7, 25) = 3.55$, $p = .009$, $MSE = 0.002$. Supporting lateral inhibition, polynomial contrasts revealed a slight quadratic trend across the lag positions ($p < .05$ for Phase 2; $p = .06$ for Phase 3). However, the pattern was not perfectly quadratic, owing to the expected rise in errors at the lag +1 position. The quadratic function proved significant when the innermost lag positions were not considered (using only lags $\leq -4, -3, -2, +2, +3$, and $\geq +4$; ps $= .02$, .05, and .04, for the three phases).

In line with the construct of self-inhibition, orthogonal contrasts indicated that more anticipatory than perseveratory intrusions were made overall in the latter two phases ($p = .008$ for Phase 2; $p = .009$ for Phase 3). Paired comparisons between the lag −1 and +1 positions revealed that in all three phases, fewer lag −1 than lag +1 intrusions were made ($p \leq .01$, two-tailed, in all cases).

Is it necessary to have two inhibitory mechanisms at work? It is possible that the graded nature of the negative-lag function arises from the decay of self-inhibition (e.g., Henson, 1998). However, the self-inhibition mechanism alone would not account for the increasing intrusion error rate observed from lag +2 to lag $\geq +4$, $t(31) = 2.14$, $p < .05$ (all other contrasts were nonsignificant). Given that we obtained both quadratic trends (greater error rates at extreme lags in both directions) and asymmetry (more anticipations than perseverations), we propose that we have evidence for both lateral and self-inhibition, respectively.

Although our primary interest is in the pattern of intrusion errors, it is notable that the accuracy of target responses was consistently high (M omission error rates $= .01$, .04, and .01, for Phases 1–3, respectively), suggesting that participants were functioning well at this task. It is conceivable that our pattern of intrusion errors was driven by a disproportionately greater availability of the end goals (1 and 7) compared with the other goals. If so, we would expect faster responses to these items (a significant serial position effect). To address this possibility, we analyzed the median correct response latencies in a repeated measures analysis of variance using the seven goal categories (Table 1). At each phase of the study, there was a strong effect of serial position, Fs$(6, 26) = 4.51$ to 6.24, all ps $< .01$. However, post hoc orthogonal contrasts indicated that these effects were driven in each case by significantly longer latencies at the Goal 1 position than at all others (ps $\leq .0001$). We attribute this pattern to the start-up time required at the beginning of each trial, and not to the greater availability of end goals.

DISCUSSION

In this study, we aimed to simulate sequential behavior in a laboratory task that incorporated the requirements of order, situation monitoring, and distraction from competing goals. We sought to find evidence for lateral and self-inhibition as two possible processes of sequential-action regulation. Across variations in presentation rate and stage of training, our analyses of intrusion errors suggest that inhibition spread laterally to neighboring goals in the sequence, but that it did not spread evenly across all seven goals. Participants made more anticipatory than perseveratory intrusions, and, in particular, they mistakenly responded to stimuli one goal ahead of the current goal (lag +1 errors). Notably, the error rates for the lag +2 position were consistently similar to those in the lag −1 position. Our functional interpretation of this pattern is that the $n + 1$ goal is the next most accessible goal relative to the present one. However, to avoid confusion with other intended actions, the system suppresses all other future goals in the same way as it suppresses completed goals via lateral inhibition.

Our findings are in agreement with the asymmetry predicted by models of sequential action (self-inhibition: e.g., Houghton, 1990) and recent findings from prospective memory research (Goschke & Kuhl, 1993; Marsh et al., 1998, 1999). Compared with previous work, the present study reveals that lateral inhibition is not as strong at extreme lags as at the innermost lags, as indicated by the relative increase of intrusions at both ends of the lag function. This pattern suggests that lateral inhibition is limited in its breadth or span. We note that a pilot study in which we used only four goals generated a lag function more similar to that reported by Houghton et al. (1994), in that intrusion errors did not rise toward the ends of the lag function. Perhaps lateral inhibition can accommodate a span of four goals. Rather than directly

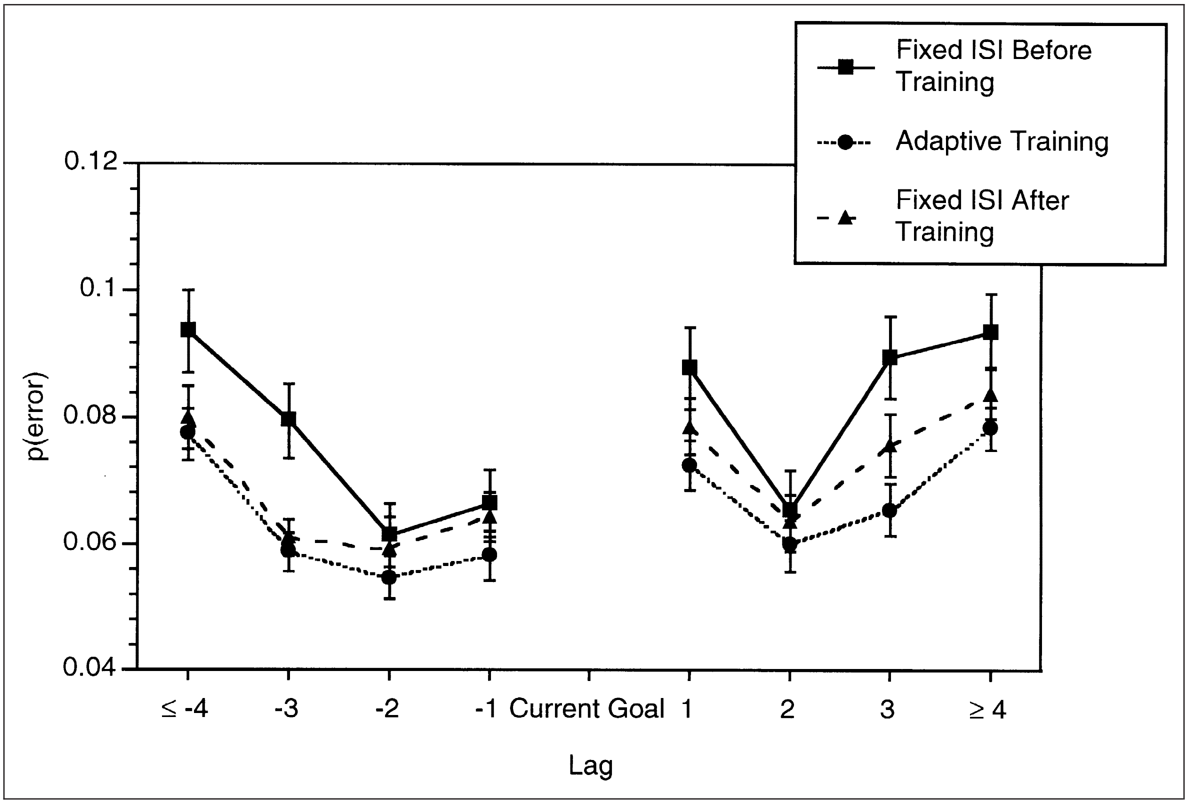

Fig. 3. Intrusion error rates by phase and lag number. Error bars represent one standard error of the mean. ISI = interstimulus interval.

comparing our results with those from spelling or serial recall tasks, we presently adopt the principles of lateral and self-inhibition and acknowledge that task differences (e.g., presence of distraction, definition of errors) may determine whether both lateral and self-inhibition are required.

In contrast to models that involve inhibitory mechanisms, alternative activation-only or spotlight models predict that intrusion errors would monotonically decrease with increasing ordinal distance from the current goal. The present data do not lend support to such alternative views, but rather, suggest the need to consider gradients of inhibition and excitation together.

In sum, the present work offers a new method of studying sequential action that does not confound the requirements of memory for the action sequence with the requirements of regulating the action sequence. Recent work on serial recall (Vousden & Brown, 1998) suggests that the value of the inhibition parameter affects the steepness of the lag function. We are now directing our empirical work toward understanding the degree to which the shape of the lag function is

Table 1. *Means of individual median latencies by test phase and serial position (in milliseconds)*

Serial position	Fixed ISI before training		Adaptive training		Fixed ISI after training	
	M	*SD*	*M*	*SD*	*M*	*SD*
1	383.83	55.07	360.45	36.29	364.44	40.80
2	362.41	55.75	344.30	41.28	353.81	47.38
3	356.75	44.34	344.05	29.46	346.38	38.35
4	357.72	35.75	349.73	29.66	355.14	38.17
5	357.83	45.39	343.58	34.77	345.84	39.89
6	360.44	53.68	345.00	38.30	349.28	44.26
7	354.47	34.81	339.36	24.51	345.00	34.56

Note. ISI = interstimulus interval.

determined by individual and developmental differences in inhibitory efficiency and span size (cf. Maylor, Vousden, & Brown, 1999).

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