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33. The Selective Negative Priming Effect: Return to an Inhibition Account

Z. Ziv Chorev and A. Henik

Department of Behavioral Sciences and Zlotowski Center for Neuroscience, Ben-Gurion University of the Negev, Beer-Sheva, Israel

Previous studies found that negative priming (NP) depends on the presence of a conflict in the probe. We studied NP by manipulating probe conflict with minimal similarity between prime and probe. In every trial participants focused on a colored figure and named the color of the following Stroop probe. NP occurred only when the probe contained distracting information (i.e., the incongruent Stroop condition). These results do not fit explanations based on prime–probe similarity, but support accounts involving inhibition as essential to NP. We believe that the inhibition activated during prime processing appears in the probe only when it involves control processes. © 2001 Academic Press

Researchers have suggested that inhibition is mediated by frontal areas (May & Hasher, 1998). This work suggests that negative priming (NP) involves inhibitory processes and reflects an executive control.

In a typical NP experiment, subjects are presented with two successive stimuli; the prime and the probe. Commonly, subjects pay attention to one item or dimension (the target) and try to ignore distracting material. The critical trials (the ignored repetitions) have the ignored distractor of the prime as the target in the probe. The repetition of the ignored distractor slows responding relative to a control condition in which there is no prime–probe relationship.

A common explanation for NP is the *distractor inhibition account.* It assumes that during prime processing, an aspect of the distractor representation is inhibited. If this distractor appears later as a probe target, this inhibition slows down responses to the probe. However, researchers found that NP depends on the presence of a distractor in the probe. For example, in the Tipper and Cranston study (1985), there were two types of ignored repetition conditions: one required selection and one did not. NP was found only when the probe required selection. If the representation of the ignored distractor were inhibited, one would expect NP regardless of whether the related target appeared with or without a distractor. The dependence of NP on the content of the probe does not fit with the distractor inhibition idea. Hence, researchers suggested alternative explanations for NP. One of the dominant alternatives was proposed by Neill and Valdes (1992) and is known as the *episodic retrieval account.* This explanation suggests that the probe stimulus cues the retrieval of past processing episodes. If the retrieved episode includes the tag ‘‘do not respond’’ to a similar stimulus, processing of the current stimulus is slowed down. Hence, episodic retrieval is influenced by similarity between prime and probe. The absence of a distractor in the probe trial may create a sufficiently different context so that the prime’s episode would not be retrieved and would not interfere.

Recently, Milliken, Joordens, Merikle, and Seiffert (1998) proposed the *temporal discrimination account.* According to this account an attention system categorizes the probe stimulus as ‘‘old’’ or ‘‘new.’’ The response to an ‘‘old’’ probe is retrieved

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directly from memory, whereas the response to a ‘‘new’’ probe relies on a new perceptual analysis. The ignored repetition condition creates ambiguity with respect to this categorization—the probe target looks familiar enough to rule out its quick categorization as ‘‘new’’ but provides an insufficient basis for its categorization as ‘‘old.’’ This ambiguity elongates processing of the probe and results in the NP effect. According to the episodic retrieval account and the temporal discrimination framework, a necessary condition for NP is similarity between the probe and prime. The following experiment was designed to manipulate conflict in a case that presents minimal similarity between the prime and the probe.

Methodology

Participants. Twenty-two undergraduates from BGU with normal color vision and normal or corrected-to-normal visual acuity.

Stimuli. The prime was a colored circle or square. Subjects were asked to use this figure as a fixation point and not to respond to it. The probe was a Stroop stimulus, one of four Hebrew color words (green, yellow, red, or blue) in one of these colors. A congruent stimulus contained a color word in the corresponding color, an incongruent stimulus contained a color word in a noncorresponding color, and a neutral stimulus was composed of a string of one repeating letter written in one of the four colors.

Procedure. A trial began with the colored figure appearing at the center of a computer screen for 300 ms. After a blank interstimulus interval (ISI of 50 or 500 ms) this figure was replaced by a Stroop stimulus at the same location. The Stroop stimulus remained in view until the subject’s vocal response. The researcher coded the subject’s response and after an additional 1000 ms the next trial began. The prime’s color was related to the probe’s color in 25% of the trials. There were equal numbers of congruent, incongruent, and neutral trials. All variables were manipulated randomly within blocks. The NP effect was examined by the comparison of the related condition (e.g., the word green in red presented after a red square) to the unrelated condition (e.g., the word green in yellow after a red square). Conflict probes were presented by the Stroop incongruent conditions and nonconflict probes were presented by the Stroop neutral conditions.

Results

Two aspects of prime–probe relatedness are of interest: (1) Color relatedness—The relation between prime color and probe color, which is the main study of this work, and (2) Word meaning relatedness—The relation between prime color and the probe word meaning. For each aspect of the prime–probe relatedness an ANOVA followed by the relevant contrasts was performed. In the color relatedness analysis a significant Stroop effect [$F(2, 42) = 104$, Mse $= 3008$, $p < .0001$] and SOA [$F(1, 21) = 41$, Mse $= 3180$, $p < .0001$] were found. In addition, a significant two-way interaction of Stroop and Color relatedness were found [$F(2, 42) = 5.5$, Mse $=$ 488, $p < .008$]. As depicted in Fig. 1, NP appeared only in the incongruent Stroop condition [$F(1, 21) = 7$, Mse $= 1163$, $p < .016$], where the RT for a related probe was longer (774 ms) than the RT for an unrelated probe (755 ms). The word-related analysis did not include congruent conditions (word meaning and word color were the same), nor neutral conditions (which did not contain words). Thus, the ANOVA was performed only for the incongruent Stroop condition. The interaction between SOA and word relatedness was significant [$F(1, 21) = 7$, Mse $= 698$, $p < .025$]. Additional analysis revealed that at an SOA of 350 ms, RTs were shorter when the

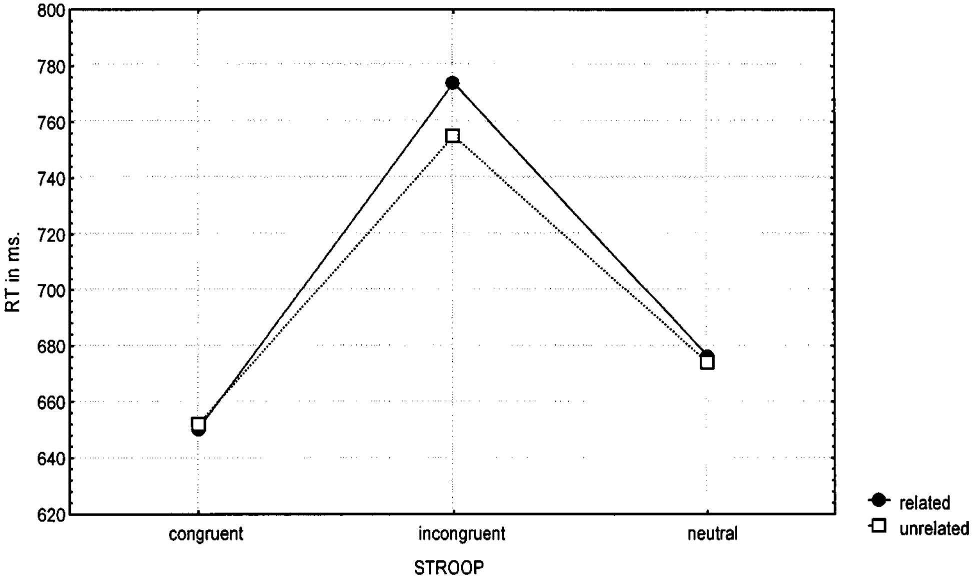

FIG. 1. Mean reaction time to color-related (circle) and unrelated (square) trials. NP effect is reflected in a slower RT to related trials than to unrelated trials. The effect occurs only in the incongruent Stroop condition.

prime (color) was related to the probe word (769 ms.) than when they were unrelated (783 ms) [$F(1, 21) = 4$, Mse $= 503$, $p < .05$].

Discussion

The results of the present study seem to be in line with those of previous studies. As expected, NP is a selective effect: it occurs only when the probe contains distracting information. Note that our experiment does not support explanations for the selective NP which are based on similarity between the prime and the probe. The prime–probe similarity is the same in the case of a conflict probe (e.g., the word blue written in red, coming after a red square) and a nonconflict probe (e.g., series of X's written in red, subsequent to a red square). According to the temporal discrimination account (Milliken et al., 1998), NP will occur when there is an ambiguity in the temporal discrimination process that categorizes the stimulus as ''old'' or ''new.'' We do not have any reason to believe that a related incongruent Stroop stimulus produced more ambiguity than an unrelated incongruent Stroop stimulus, while a related neutral Stroop stimulus was categorized as easily as an unrelated neutral Stroop stimulus. In other words, the differences in novelty between related and unrelated trials are the same for conflict and nonconflict probes. It seems that episodic memory or temporal discrimination processes cannot explain the selectivity of the NP effect in the current paradigm. We suggest that participants inhibited prime processing because they were required not to respond to the prime, and the prime's color was related to the probe's color in only 25% of the trials. The inhibition affects probe processing only when the probe requires selection. It seems that inhibition is a strategy that participants adopt during prime processing due to the experimental context that encourages it. We suggest that it might be useful to think of this selectivity effect as evidence that a conflict probe and a nonconflict probe are processed in different ways—one involves control processes and the other does not. The inhibition activated during prime processing would be reflected in responses to the probe only when the probe involves control processes.

Tipper and Cranston (1985) proposed a similar theoretical approach to explain the selectivity of the NP effect. They suggested that during prime processing the mental representation of the ignored distractor remains activated, but its access to the response mechanisms is blocked. If probe processing requires selection too, the participants will use the same ‘‘selection state’’ that was adopted during processing of the prime. We suggest that it is not a ‘‘state’’ that is adopted, but rather the involvement of a control process during probe processing, that enables the inhibition to appear and elongates the probe RT.

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34. The Central Executive Functioning: One or Several Underlying Capacities? A Study in Healthy Young Adults

S. Fournier and P. Larigauderie

Laboratory of Language and Cognition (LaCo), CNRS, University of Poitiers, Poitiers, France

The aim of this study was to investigate the hypothesis that the central executive component of working memory can be fractionated, in demonstrating that its traditionally assigned functions (coordination of activities, inhibition, retrieval from long-term memory, and planning) depend on various independent capacities. The performances of 50 young adults were examined in a range of executive tasks. A factorial analysis suggested that the subjects’ performances could be related to four domains of the executive functions: the ability to inhibit predominant responses associated with strategic retrieval from long-term memory, the ability to inhibit irrelevant information, and the capacities to coordinate storage and processing of verbal versus visuospatial information. These results are consistent with the hypothesis of the fractionation of executive functioning.

Recent theoretical and empirical attempts have been made to examine the functioning of the central executive (CE) component of working memory and to specify its functions more precisely (see in particular Baddeley, 1996). A review of the literature suggests that the CE is involved in a number of different functions: the coordination of two activities performed simultaneously, the inhibition of an ongoing response strategy which is no longer appropriate, the inhibition of a predominant response or of a response which is irrelevant to the current task, the strategic retrieval from long-term memory (LTM), and the planning of activities. Therefore, the CE has been assigned an important role in many different operations.

The aim of this study is to examine normal CE functioning in healthy young adult subjects and to demonstrate that various independent capacities are involved in the different functions traditionally assigned to the CE.

Method

Subjects. Fifty young adults (24 men and 26 women) participated in this study. All participants were either undergraduate or graduate students from the University of Poitiers. The participants ranged from 18 to 31 years old (mean age 23.5 ± 3.17 years).

Materials. We explored our hypothesis by using a range of tasks specifically selected to assess each specific aspect of executive functioning. Some of these stem from a replication of the different executive tasks available in the literature; others have been developed specifically for this study. Task selection was based on the analysis of the various control processes involved in each task. Several tasks were selected to assess the coordination function. Three types of coordination were considered: the coordination of storage and processing according to the nature of the information (verbal—verbal backward digit span—and visuospatial—visuospatial backward span), as well as the coordination of two different types of processing without storage (semantic and phonemic: ‘‘double processing’’ task) and the coordination of two different types of storage without processing (verbal and visuospatial: ‘‘double storage’’ task). In the same way, several tasks were used to assess three different aspects of the inhibitory function: the inhibition of a predominant response (random letter generation task, Hayling test), as well as the inhibition of previous response strategies (Wisconsin Card Sorting Test, Trail-Making test) and the inhibition of irrelevant information (Stroop test). The retrieval function was assessed by verbal fluency tasks (semantic and phonemic) which are typically associated with strategic retrieval processes from LTM. The last group of tests assessed the planning function; these tests employed either verbal material (arithmetic problem solving task) or visuospatial material (maze task).

Results and Discussion

A factorial analysis was carried out and four factors emerged with eigenvalue >1, accounting for 67.21% of the variance. The eigenvalues for the four factors were 2.3, 1.74, 1.34, and 1.32, respectively (see Fournier and Larigauderie, in preparation). The tasks loading heavily on factor 1 were the Hayling test (B-A time), the fluency task (number of words generated on both phonemic and semantic fluency) and the random letter generation task (global score). Correct performance on these tasks requires the ability both to inhibit a predominant response (that can be automatically activated in working memory) and to develop a strategic search and retrieval process from LTM. In the Hayling test subjects must complete a sentence with a word which is unrelated to that sentence. Such a task requires the inhibition of the expected word, but it also requires a strategic search in LTM to produce a word that fits the instructions. In a similar way, the verbal fluency task requires the inhibition of the usual search strategy on the basis of the meaning of the word, while carrying out a strategic retrieval from LTM in order to access new items. Finally, performing a random generation task requires the subjects to inhibit the natural tendency to produce letters in the alphabetical order and also requires a strategic search and retrieval from LTM (for instance, to produce a letter that does not follow the one that has just been produced). Thus, this first factor can be interpreted as reflecting the ability to inhibit automatically activated information associated with strategic retrieval from LTM. Factor 2 is made up of the performance on the two Stroop interference conditions;

under those two conditions, subjects have to select the relevant information from two choices which clearly requires the inhibition of irrelevant information. Thus, this second factor can be associated with the capacity to inhibit irrelevant information when several options are present. The third factor is made up of the performance on the verbal backward digit span task and the arithmetic problem solving task. The verbal span task requires the storage of sequences of digits while manipulating the retained information in order to repeat the sequences in reverse order.

As we analyze the processes implied in the arithmetic task, we find that this task also requires the subjects to retain verbal information (the problem's data) while performing a computation, which means mentally manipulating the retained information. Therefore, this factor can be related to the ability to coordinate storage and processing of verbal information. The last factor is made up of the performance on the visuospatial backward span task and the maze task. The visuospatial span task involves touching colored squares depicted on a test card in reverse order of presentation, which requires the subjects to retain sequences of ''touching'' and to manipulate the retained information in order to repeat the sequences in the reverse order. The maze task was previously selected to assess the ability to plan a visuospatial activity; however, this task also requires the maintenance of visuospatial information (the path which is currently tested by the subject) while processing this retained material. This factor can be related to the capacity to coordinate storage and processing of visuospatial information.

Taken as a whole, the results are consistent with the hypothesis of the fractionation of executive functioning. The emergence of four factors suggests that various capacities contribute to the performance in the selected executive tasks. Globally, the coordination function does not seem to rely on a general capacity; distinct capacities could be involved when simultaneously coordinating storage and processing, when coordinating two types of processing, or when coordinating two types of storage. Our data suggest that the coordination function could depend on at least two separate capacities according to the nature of the retained and/or processed information (verbal vs visuospatial). This point is consistent with Baddeley's conception of a CE working interactively with two slave systems, each specialized in the storage of verbal vs visuospatial information. Moreover, these two capacities are also distinct from the ability interpreted as reflecting retrieval and inhibition processes. Indeed, these two processes can not be dissociated in the three tasks loading heavily on the corresponding factor (Hayling test, verbal fluency and random generation). In the literature, the relation between these tasks is traditionally interpreted as reflecting the important inhibition demand associated with them (see Baddeley, 1998, for an interpretation of the relation between the verbal fluency and the random generation tasks; see Collette et al., 1999, for an interpretation of the relation between the verbal fluency task and the Hayling test). However, we can hypothesize that strategic retrieval from LTM is closely linked to the necessity to inhibit automatically activated information, as if the deactivation of the current representation was a necessary step in accessing and retrieving new items. This point of view is consistent with the retrieval model recently proposed by Rosen and Engle (1997). Finally, this former factor is independent from another factor made up by the interference score on the Stroop task which is typically associated with the inhibition of irrelevant information without implicating retrieval processes. These data lead us to consider two types of inhibitory mechanisms: inhibitory mechanisms associated with strategic retrieval processes, assigned to prevent nonselected information from interfering with the processing; and inhibitory mechanisms associated with information selection which are in charge of inhibiting distracting information. This is supported by the fact that when we examine subjects' performance on factor 1 (capacity to inhibit predominant responses associated with strategic retrieval), on the basis of a contrast on verbal fluency performance for instance, we notice that the performance of the ‘‘high capacity’’ group and the ‘‘low capacity’’ group on the three tasks loading most heavily on this factor are significantly different. On the other hand, no significant differences are observed between these two groups concerning the capacities related to the other factors including factor 2 which is associated with the inhibition of irrelevant information.

Conclusion

In summary, this study suggests that various aspects of executive functioning depend, at least partly, on distinct capacities which imply the independence of some control processes. To conclude, the CE component of working memory should be conceived more as a combination of capacities (each of them determined by interactive but partially independent control processes) rather than as a unitary system in which the various control functions depend on a single general capacity.

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35. Cognitive Processes Underlying a Frontally Mediated Component of Task Switching

A. Gotler and N. Meiran

Department of Behavioral Sciences and Zlotowski Center for Neuroscience, Ben-Gurion University of the Negev, Beer-Sheva, Israel

Preparing for a task switch reduces but does not eliminate behavioral switching cost. Converging evidence from cognitive, functional neuroimaging, neuropathology, and aging research indicates that (a) cost is reduced by preparation and (b) remaining (residual) cost represents distinct processes, with residual cost uniquely related to prefrontal functioning. De Jong (2000) claimed that residual cost reflects a failure to engage in advance task preparation in some trials. We found that strongly encouraging advanced preparation by withdrawing the cues indicating which task to execute did not affect residual cost. The results support the claim that residual cost is associated with updating response-related information in working memory (Meiran et al., 2000), taking place in the prefrontal cortex.

Switching tasks is associated with a cost in performance. This switching cost diminishes when participants are given time to prepare for the next task (e.g., De Jong, 2000; Kramer, Hann, & Gopher, 1999; Meiran, Chorev, & Sapir, 2000; Rogers et al., 1998). Switching cost, which is eliminated by preparation, was called by Meiran et al. the ‘‘preparatory component.’’ However, even when given ample time to prepare, switching cost is not eliminated, and the remaining switching cost is called ‘‘residual cost.’’ The two components involve different cognitive processes (Meiran et al.) and different brain structures. Most notably, the residual component seems to involve the prefrontal cortex. It is elevated after focal frontal lesions (Rogers et al.), in the elderly (Kramer et al.), and is associated with elevated blood oxygenation level-dependent (BOLD) responses in the dorsolateral prefrontal cortex (DLPFC) in normal young participants (Dove et al., 1999). In contrast, the available evidence does not suggest frontal involvement in the preparatory component. This component of switching cost is normal in the elderly (Kramer et al.), at least when explicit instructional cues indicate which task to perform. Moreover, Dove et al. were unable to identify significant instructional cue-locked BOLD responses in the prefrontal cortex.

For these considerations, better understanding of the cognitive processes underlying the residual component will contribute to our understanding of prefrontal functioning. An interesting explanation was offered by De Jong (in press), where he claimed that when participants do prepare for task switching, the residual cost is eliminated. However, in some trials they do not engage in advanced preparation, but wait until the target stimulus is presented. This mixture of prepared and unprepared trials gives rise to the residual cost.

In the present experiments, participants were required to indicate the location of a target stimulus (smiling face) within a 2 × 2 grid. Two tasks were ordered randomly. One task involved UP vs DOWN discrimination (ignoring the horizontal dimension), while the other task involved RIGHT vs LEFT discrimination (ignoring the vertical dimension). Prior to the presentation of the target stimulus, the participants were instructed, by means of a symbolic instructional cue, which task to perform. In order to separate the two components, we manipulated the cue–target interval (CTI), which is the time allowed for preparation. In this design, switching cost at the longest CTI indicates the residual component.

If the residual cost were only due to trials in which advanced preparation failed, one would predict it would be eliminated in conditions where correct responding depends on successful advanced preparation. In order to manipulate participant’s engagement in advance preparation, we created two conditions. In one condition, the instructional cue remained visible until the participant responded, and in the second condition, the cue was withdrawn as soon as the target stimulus was presented. In this condition, participants could not maintain a reasonable error rate without advanced preparation. We reasoned that preparation would begin with cue processing and would not be delayed until target presentation because task preparation is less efficient in the absence of strong instructional cues (see Rogers et al., 1998, regarding weak and strong cues).

Method

Participants. Sixteen undergraduate students participated in a 1-h session. The participants responded by pressing keys on the numeric pad of the keyboard. Half of them were randomly assigned to respond with the top-left key, indicating UP or LEFT depending on the task and bottom-right key, indicating DOWN or RIGHT. The other half used the bottom-left key and the top-right key.

Procedure. There was a short warm-up session (20 trials) and four experimental blocks (140 trials each). In each trial, the CTI task and target position were randomly selected. Each trial consisted of (a) the presentation of an empty grid for fixation for

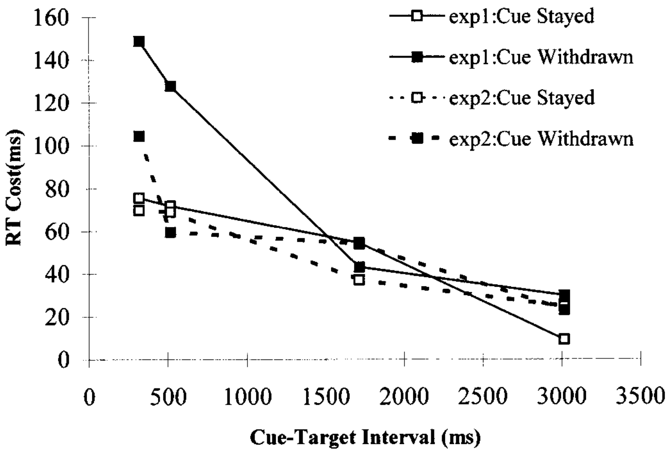

FIG. 1. Task-Switching cost (switch RT minus no-switch RT, ms) as a function of condition.

1516 ms, followed by (b) the instructional cue presented for a variable CTI (316, 516, 1716, 3016 ms). In the cue-withdrawal condition, this was followed by the presentation of the target stimulus until the response. In the cue-stay condition, the instructional cue remained visible until participant's response.

Results and Discussion

The results showed that withdrawing the cue increased the preparatory component which indicates that participants were, in fact, encouraged to engage in advance preparation. Moreover, cue withdrawal did not significantly affect the size of the residual component, with a trend in the opposite direction (see Fig. 1).

RT. Preparation significantly reduced switching cost, indicated by the two way interaction between CTI and Task Switch [$F(3, 42) = 14.18, p < .0001$]. Importantly, the simple main effect of Task Switch at the longest CTI was significant [$F(1, 14) = 7.57$, $p < .01$, $MSE = 6064.51$], indicating a residual switching cost. The triple interaction between CTI, Task Switch, and Cue Withdrawal approached significance [$F(3, 42) = 2.66$, $p = .06$, $MSE = 2134.70$]. This interaction reached significance in an analysis which included only the shortest and the longest Cue–Target Intervals [$F(1, 14) = 5.29$, $p < .05$], indicating a larger preparatory component in the Cue-Withdrawal condition. The difference in the size of the switching cost in the longest CTI did not approach significance, which means that cue withdrawal did not significantly affect the residual cost.

Experiment 2

In the cue-withdrawn condition, the participants were placed under heavier memory demands, being forced to respond while holding cue information in memory. In other words, the cue-withdrawal manipulation confounded two variables, encouraging advance preparation and memory load during target processing. So both the larger preparatory component and the existence of the residual could be the result of the increased memory load. Therefore, in Experiment 2 we manipulated Cue Withdrawal randomly within a block of trials. Since, when the cue was presented, the participants could not predict if it would be withdrawn, they were presumably equally encouraged to engage in advance preparation in each and every trial. Of interest is the condition where the cue stayed. In this condition, participants were strongly encouraged to engage in advance preparation, but were not placed under heavier memory demands when processing the target stimulus.

Method

Fourteen participants participated in Experiment 2 in a single 1-h session. Cue withdrawal was manipulated randomly within subject; otherwise the experiment was the same as Experiment 1.

Results

The results were treated in the same way as in Experiment 1. First, Cue Withdrawal, that manipulated memory load only, did not significantly affect the size of the preparatory component, giving more strength to the findings in Experiment 1. Second, residual Task Switching was equal in the two Cue-Withdrawal conditions and highly significant.

RT. Preparation reduced switching cost, indicated by the significant interaction between Task Switch and CTI [$F(3, 39) = 8.80$, $p < .001$]. The triple interaction between CTI, Task Switch, and Cue Withdrawal was not significant this time. We also tested the simple main effect of Task Switch at the longest CTI and found it to be significant, indicating a residual cost [$F(1, 13) = 11.49$, $p < .005$]. As in Experiment 1, Cue Withdrawal did not affect the residual cost [$F < 0.1$].

Errors. Error rate was extremely low. Most notably, it was less than .005 in the longest CTI, and there was no indication of speed accuracy tradeoff. The low error rate indicates that cue information was processed.

General Discussion

Cue withdrawal increased advanced preparation but did not reduce the residual cost. Therefore, we argue that failing to engage in advanced preparation is not the only reason for residual costs. However, we agree with De Jong that such a failure (a) may take place in some situations and (b) would increase residual costs.

The evidence that different brain mechanisms are responsible for the two components of switching cost is also not easily explained by De Jong's (2000) model. The reason is that the model attributes switching cost to a single process of task preparation. We suggest that a more plausible account is that task switching is associated with directing attention to the relevant stimulus dimension, mediated by posterior and subcortical brain mechanisms, and reflected in the preparatory component of switching cost. In addition, task switching is also associated with updating response-related information in working memory, taking place in DLPFC, reflected in residual costs (e.g., Meiran et al., 2000, for relevant references).

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36. Human Premotor Cortex, not Prefrontal Cortex, Is the Site of Spatial Working Memory

D. V. Meegan

Department of Brain and Cognitive Sciences, University of Rochester

It is widely assumed, based largely on macaque research, that dorsolateral prefrontal cortex is the critical area for spatial working memory (SWM) in humans. I present a metaanalysis of functional neuroimaging studies which shows instead that dorsal premotor cortex (BA 6) is the most consistently activated area when spatial information must be ''kept in mind'' for short periods. I suggest that mnemonic mechanisms for planning spatial movements are recruited for spatial maintenance in nonmotoric tasks. I contrast this explanation with two alternative explanations for premotor activation: (1) the area of activation is not a premotor area and (2) the area of activation is the frontal eye field.

At the beginning of the functional neuroimaging revolution, many researchers were surprised by prevalent activation of motor areas such as the cerebellum, basal ganglia, and frontal motor areas during many cognitive tasks. In the case of the cerebellum, the initial surprise has matured to an effort to explain what common underlying process might be recruited by both cognitive and motor tasks. Another surprise has been the activation of premotor cortex (BA 6) during SWM. In this case, however, the initial surprise seems to have led to a decision to ignore a finding that cannot be reconciled with existing theory. My goal is to do for premotor cortex what others are doing for the cerebellum, by attempting to understand its role in both cognitive and motor tasks.

There is much evidence to suggest that the principal sulcus region (BA 46) of the macaque dorsolateral prefrontal cortex plays a critical role in SWM. For this reason, the first human neuroimaging investigations of SWM expected that a homologous area of dorsolateral prefrontal cortex would be active. The first published study, by Jonides et al. (1993), failed to find any activity in this area. However, they, and many investigators since, have consistently found activity in dorsal premotor cortex, in and around the caudal portion of the superior frontal sulcus. Dorsolateral prefrontal cortex has been active in some SWM tasks, but specifically those that have required some manipulation of spatial information in addition to basic mnemonic maintenance. Note the consistency with Baddeley's view of working memory—the ''central executive'' may be located in prefrontal cortex and the ''visuospatial sketchpad'' may be located in premotor cortex.

I suggest that the role of premotor cortex in SWM is related to its role in motor control. Understanding this suggestion is made easier by comparing it to the accepted view of verbal working memory (VWM) or Baddeley's ''phonological loop.'' When one keeps verbal information in mind through a delay period, it is thought that the information is rehearsed with an ''inner voice.'' In other words, neuromotor mechanisms for speech are utilized for mnemonic maintenance. This view has been supported by neuroimaging findings, as premotor speech centers (i.e., Broca's area) are active during VWM. In summary, the role of premotor cortex in VWM is related to its role in motor control.

Dorsal premotor cortex plays a role for spatial/skeletal movements similar to the role Broca's area plays for speech/orofacial movements—it is involved in the cognitive aspects of motor control, such as planning. In addition, dorsal premotor cortex receives inputs from sensory and association areas and uses this information for planning sensory-guided movements. An essential part of motor planning is being able to keep multiple components of complex action sequences ''online.'' In the case of spatial movements, such a process entails maintaining a spatial representation of movement targets in sensorimotor coordinates. Now consider that such a motor control mechanism could also maintain a spatial representation of sensory targets, even when no movements are made to those targets. I suggest that this is the function of dorsal premotor cortex in SWM.

There is also behavioral evidence for a premotor contribution to maintenance in SWM tasks. In Brooks' classic spatial imagery task, a task that is heavily dependent on SWM, performance is disrupted specifically when humans are required to make movements that are spatially incompatible with the imagined object. Logie (1995) reviews additional findings in which SWM performance is impaired when humans are required to make movements that are spatially incompatible with the information to be remembered.

Although most frontal lobe researchers continue to espouse the view that dorsolateral prefrontal cortex is the primary site for SWM in the human brain, some have attempted to explain the BA 6 activation in SWM tasks. Courtney et al. (1998) suggest that the cytoarchitectonic classification of the superior frontal sulcus region has mistakenly identified it as agranular (premotor) cortex instead of granular (prefrontal) cortex. Although I am not a neuronanatomist, I am comfortable that important figures such as Brodmann and Talairach would not have made such an error. Zarahn et al. (1999) have identified the area of activity in SWM as the human frontal eye field and (like me) suggest a role for a motor area in nonmotoric tasks. I disagree with Zarahn et al. on two grounds. First, when BA 6 activity from SWM studies is plotted on a Talairach brain, the points of activity clearly follow the superior frontal sulcus, with some points near the junction with the precentral sulcus. In contrast, when activity from eye movement studies is plotted, the points of activity clearly follow the precentral sulcus, with some points near the junction with the superior frontal sulcus. Second, although eye movements are spatial movements, they are unable to specify three-dimensional space as thoroughly as skeletal movements. Smith and Jonides (1999) have suggested that the BA 6 activation reflects the recruitment of covert attention, which is used to shift among to-be-remembered locations. In support of this view they cite imaging studies of spatial attention in which similar BA 6 activation is found. One thing that is often overlooked about many spatial attention tasks is that they are actually spatial memory tasks—a location is cued and a target subsequently appears at the cued location following a delay period. So, in contrast to Smith and Jonides, I suggest that BA 6 activations in both memory and attention tasks are due to the spatial memory requirements of the tasks.

Human frontal lobe researchers have not been able to reconcile the role of dorsal premotor cortex in cognition with its role in motor control. Although I hope my suggestion is correct, I am more concerned that frontal lobe researchers begin to appreciate that understanding the role of the frontal lobes in cognition may require an understanding of their role in motor control. To make matters more complicated, the supplementary motor area (the medial portion of BA 6) has also been active in many working memory studies. Although I do not offer an explanation for the role of SMA in working memory here, I suggest a similar approach to the one that has been adopted to explain the cognitive functions of other motor areas such as cerebellum, basal ganglia, and dorsal premotor cortex.

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37. An Evaluation of Models of the Topographical Organization of Working Memory Function in Frontal Cortex with Event-Related fMRI

R. Bradley, A. Postle, and M. D'Esposito

Department of Neurology, University of Pennsylvania Medical School

Many models of the organization of working memory function in prefrontal cortex have been developed and/or tested with functional neuroimaging methods featuring the blocking of behavioral trials and the averaging across blocks of neuroimaging signal. Interpretation of the results of these first generation neuroimaging studies, however, is subject to several inferential constraints. We reassessed several models of the functional organization of working memory in prefrontal cortex by examining or reanalyzing data from event-related fMRI studies of working memory function that were not subject to the same inferential constraints. This process permitted us to reject some of the models derived from first generation neuroimaging data, to refine others, and to synthesize our results into a revised hybrid model of the working memory functions of prefrontal cortex.

Neuroimaging studies of the working memory functions of the prefrontal cortex (PFC) have been an important source of data from which current models of the organization of mnemonic functions of PFC have been constructed. The models that we considered in this project can be classified into two broad categories—those that emphasize organization by stimulus material and those that emphasize organization by process.

Organization-by-stimulus-material models were motivated by Goldman-Rakic's (1987) modular organizational scheme for PFC, with anatomically discrete regions of PFC supporting working memory processing in a fashion that preserves the segregation of material-specific sensory processing areas. Organization-by-process models, in contrast, were preceded by Petrides' proposal that working memory functions of lateral PFC are organized into two stages, with ventrolateral areas 12/47 and 45 supporting computationally simpler executive functions such as the active comparison and assessment of stimuli represented in working memory and middorsolateral areas 9 and 46 supporting the computationally more complex functions of monitoring actions in the recent past and/or the number of stimuli represented in working memory and their relevance for behavioral objectives (Petrides, 1994).

The neuroimaging studies that have given rise to these models can be viewed as belonging to the first generation of neuroimaging methods. Interpretation of data acquired with these methods must be tempered by several inferential constraints that accompany the methods with which block-design data are typically processed and analyzed. Noteworthy among these methods are: (1) the averaging of neuroimaging signal across a block of trials; (2) the ‘‘cognitive subtraction’’ of signal from two matched blocks of trials; (3) the spatial smoothing of data; (4) the spatial normalization of data; and (5) the use of fixed effects models in group analyses. The accompanying inferential constraints include, respectively: (1) the inability to isolate neuroimaging signal ascribable to theoretically dissociable mental processes; (2) the unreliability of the assumption of pure insertion upon which many cognitive subtraction designs depend; (3) the loss of spatial resolution due to smoothing; (4) the implicit assumption behind the spatial normalization of data of precise topographical correspondence of functional specialization across participants; and (5) the inability to generalize the results of analyses employing fixed effects models beyond the individual participants comprising the sample.

Thus, the conclusions drawn from a first generation neuroimaging study of, say, performance on the *n*-back working memory task, may be limited because of the inability to resolve the discrete contributions to neuroimaging signal of the mnemonic processes of storage and maintenance of items in working memory from the nonmnemonic control processes of shifting attention, mediating proactive interference, and coordinating multiple task performance. Furthermore, in some cases the conclusions drawn from first generation neuroimaging studies may be inaccurate, due to failures of cognitive subtraction. The recent development of event-related fMRI techniques has provided a second generation of neuroimaging methods to which many of the shortcomings that characterize the first generation of PET and fMRI methods do not apply. We used an event-related fMRI design and analysis method permitting assessment of the variance in the fMRI signal attributable to each of these components of the delayed-response trial, uncontaminated by variance attributable to the other trial components, to reassess models of frontal lobe working memory functions derived from first generation neuroimaging studies.

Methods

Participants

Participants in each of our studies were healthy, unmedicated young adults. Six participants performed a spatial/object delayed-response task, and two separate studies of delayed response with letter stimuli featured seven and five participants, respectively.

Behavioral Tasks

Spatial/object-delayed response. This task employed a ‘what-then-where’ design, with an object and a spatial delay period incorporated in each trial (Rao et al., 1997).

Letter-delayed item recognition. Each trial of this task presented sequentially the memory set, initial delay, instructions (‘‘Forward’’ or ‘‘Alphabetize’’), principal delay, and a letter-digit probe. The probe assessed memory for item position on ‘‘Forward’’ trials and for relative position in the alphabet of an item on ‘‘Alphabetize’’ trials.

FMRI Procedure

Data for each of our event-related fMRI experiments were acquired on a 1.5-T scanner. Our inferential statistics were derived using multiple regression. We modeled the fMRI signal changes occurring during each qualitatively distinct component of the behavioral trials (i.e., *target*, *delay*, *probe*) with a series of covariates that were entered into a modified general linear model (GLM) for autocorrelated observations. Each covariate comprised a hemodynamic response function positioned appropriately to represent neural activity associated with one of the task components.

Results

Functional Organization by Stimulus Material

Dorsolateral and ventrolateral regions of frontal cortex may differentially support working memory for spatial and object stimuli, respectively. The results of our event-related fMRI experiment failed to generate evidence, in single participant analyses and in a relative effect size group analysis, for anatomical segregation of spatial and object working memory function in frontal cortex. Additionally, the single-participant analyses that we performed for the present report did not show any reliable evidence for a systematic segregation of object- and spatial-related activity attributable to either the target or the probe components of the task.

Left and right middorsolateral PFC may differentially support working memory for spatial and object stimuli, respectively, and left and right ventrolateral PFC may differentially support working memory for spatial and object stimuli, respectively. The results of our group analyses revealed no reliable lateralization effects in areas 44/45 or 9/46 or the SFS ROI and a suggestion of a lateralization trend in area 47, with object-delay period activity lateralized to the left hemisphere and spatial to the right.

Working memory for verbal material may be preferentially processed in the left hemisphere of PFC. We performed normalized voxel count group analyses on the data from all 12 participants in the letter-delayed item-recognition tasks. The group lateralization data indicated that there were no reliable lateralization effects in areas 9/46 or area 47, but a significant effect of more left-than-right hemisphere activity in area 44/45.

Functional Organization by Process

Dorso- and ventrolateral PFC may, to the relative exclusion of other mnemonic processes, support manipulation and maintenance, respectively, of items held in working memory. We assessed this model with data from the *letter-delayed item-recognition* task. Previously published data from each participant in both studies revealed a reliable effect of greater alphabetization-related-then-maintenance-related activity in dorsolateral PFC. The model in question would predict that maintenance-related activity within these same 12 participants would be greater in ventrolateral PFC than in dorsolateral PFC. We tested this model by performing a normalized voxel count analysis on data from these 12 participants in which we assessed the proportion of voxels sensitive to maintenance across the delay of five items in ‘‘forward’’ order in each of the three PFC ROIs. The ANOVA revealed no effect of ROI [$F(2, 22) = 1.22$; Fig. 1].

Discussion

The process of reassessing models of PFC working memory function has permitted us to reject some of the models derived from first generation neuroimaging data and to refine others. It also presented us with an opportunity to synthesize what we have learned into a revised model of the working memory functions of PFC:

1. Processes supporting working memory maintenance of verbal information are left-lateralized in ventrolateral PFC areas 44 and 45.

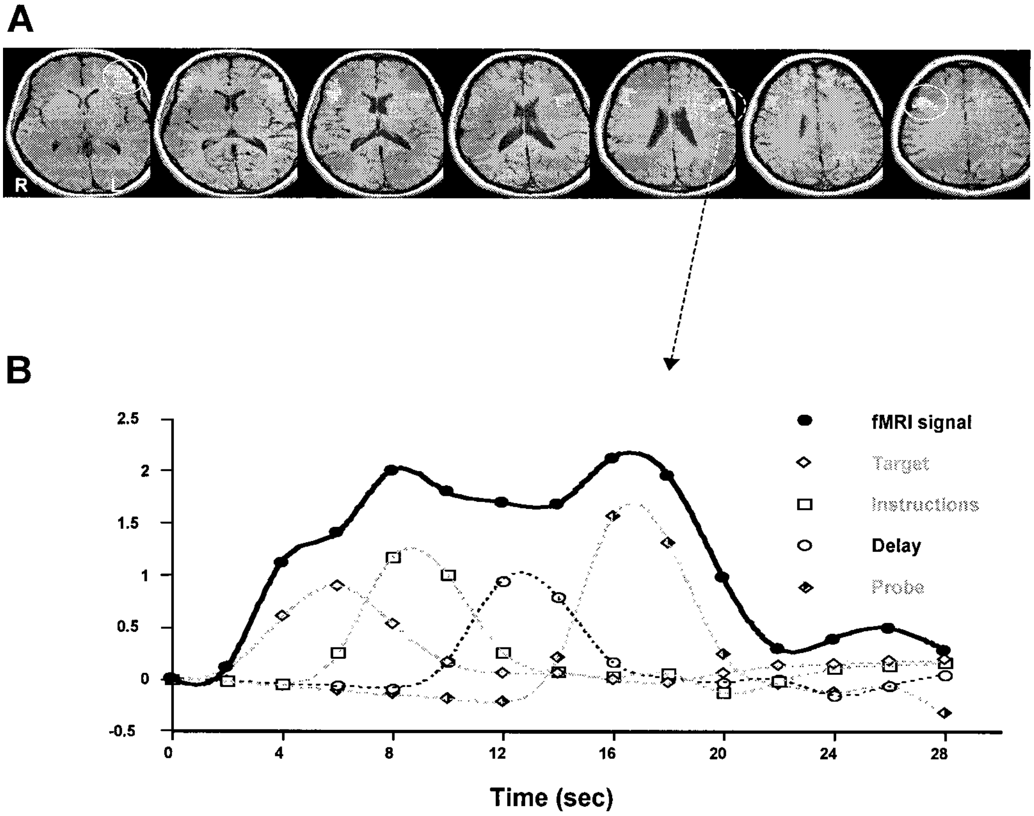

FIG. 1. Significant delay-period activity (white voxels) during Forward 5 trials in areas 44/45 in Participant #1. Dotted circle identifies voxels in Brodmann's area 44 whose time series is depicted in panel B. (B) Trial averaged time series, average across the four voxels identified in panel A. Inspection of covariates, scaled by their parameter estimates from each of the four distinct components of the delayed item recognition task illustrates that these voxels were significantly active during all components of the trial, not just the delay period.

2. Processes supporting working memory maintenance are nonetheless broadly distributed, because dorsolateral PFC is activated by these processes to an extent comparable to ventrolateral PFC.
3. Processes supporting working memory maintenance of spatial and nonspatial visual stimuli are also broadly distributed, and they only dissociate to a subtle degree in anterior ventrolateral area 47, where object maintenance may be preferentially left lateralized and spatial maintenance may be preferentially right lateralized.
4. The processes supporting manipulation of information held in working memory are largely confined to dorsolateral PFC, bilaterally.

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38. Effects of Local and Global Context in a Spatial–Numeric Stroop Task

R. West and S. J. Crewdson

Department of Psychology, University of Notre Dame

The effects of local and global context on selective attention were examined in a Stroop-like paradigm placing numeric identity and spatial location in opposition. The results of Experiment 1 revealed that spatial location interfered with the identification of numeric identity, while numeric identity had no effect on the identification of spatial location. In this experiment local task context modulated response latency for congruent trials and had little effect on response latency for incongruent trials or response accuracy. In Experiment 2, the magnitude of the interference effect was modulated by global task context and this effect was reflected in both response latency and response accuracy. The findings of these experiments indicate that different processes support to the effects of local and global context on selective attention.

The ability to selectively attend to one source of information while disregarding another source of information represents the defining characteristic of selective attention. Over the past 40 years much has been learned about the nature of selective attention and a number of important variables that influence the efficiency of this faculty identified including the processing demands of task, the global context within which the task is performed, and the functional integrity of the prefrontal cortex (LaBerge, 1995).

The Stroop task (MacLeod, 1991), where individuals are instructed to name the color of a compatible (e.g., RED presented in red) or incompatible word (e.g., RED presented in blue), has been used to study the effects of global task context on the efficiency of selective attention. Findings from a number of studies have demonstrated that the magnitude of the interference effect decreases as the proportion of incongruent trials increases (Lowe & Mitterer, 1982). These data indicate that selective attention can be flexibly allocated in response to the global contextual demands of a situation.

What is less well understood is the degree that selective attention is influenced by the moment to moment contextual demands of a performed task. Gaining a clearer understanding of the influence of local context on the efficiency of selective attention is warranted given data from a growing number of studies indicating that the efficiency of selective attention fluctuates in a dynamic fashion over the course of task performance and that the frequency or amplitude of these fluctuations increases in individuals with reduced attentional resources (e.g., older adults and individuals under divided attention; West, 1999).

The goals of the current study were threefold: (1) to introduce a previously unstudied variant of the Stroop task placing the numeric identity and spatial location of a stimulus in opposition: the development of this task may be useful in the study of interference effects in individuals who have spoken language deficits that would prohibit use of the standard vocal color-word version of the task; (2) to examine the possible influence of local context on the performance of this task; and (3) to examine the influence of global task context in this task to ensure that the observed interference effect responds to a well-characterized experimental manipulation.

Method

Participants. Eighty (40 in Experiment 1 and 40 in Experiment 2) University of Toronto undergraduates provided informed consent and received course credit for their participation.

Materials and procedure. The stimulus display was made up of four horizontally aligned boxes measuring 22 × 18 mm and outlined by two white rectangles presented on a black background. The boxes were separated by 4 mm making the display 100 × 18 mm. The boxes were mapped to four keys of a computer keyboard (box 1 = v, box 2 = b, box 3 = n, and box 4 = m). On a given trial the digit 1, 2, 3, or 4 appeared in one of the four boxes. Stimuli were presented until a response was made followed by the next stimulus 200 ms later.

In the *digit* identification task participants pressed the key corresponding to the identity of the digit. In the *spatial* location identification task participants pressed the key corresponding to the location of the digit. For congruent trials the identity and spatial location of the digit were the same (e.g., a *2* presented in the second box). For incongruent trials the identity of the number and its spatial location did not match (e.g., a *2* presented in the third box).

In Experiment 1 participants performed two blocks (145 trials per block) of the digit task and two blocks of the spatial task. The order of the tasks was counterbalanced across individuals. Performance was measured on 144 trials, with the additional congruent trial serving to establish the first trial pair. Seventy-three trials in each blocks were congruent (C) and 72 were incongruent (I). The effect of local context was established by forming four types of trial pairs (C*C,* I*C,* I*I,* C*I*), where response latency and accuracy for the second item of the pair provided the measure of interest. Participants completed 20 practice trials before each task.

In Experiment 2 the proportion of congruent and incongruent trials was varied between blocks of trials to examine the effect of global context on the digit task. For the two mostly congruent blocks there were 108 congruent trials and 36 incongruent trials. For the two mostly incongruent blocks there were 108 incongruent trials and 36 congruent trials. The order of the mostly congruent and mostly incongruent blocks of trials was counterbalanced across participants. Participants completed 20 practice trials before the first block of mostly congruent trials and the first block of mostly incongruent trials.

Results

Experiment 1. The response latency data (RL) were analyzed in a 2 (task, digit space) × 4 (condition, CC, IC, II, CI) × 2 (order) ANOVA. The effect of task was highly significant [$F(1, 38) = 288.63$, $p < .001$], with RL being faster in the spatial ($M = 453$ ms) than digit ($M = 609$ ms) task. The main effect of condition was also significant [$F(3, 114) = 76.10$, $p < .001$], with RL being faster for congruent trials (CCM, 505 ms; ICM, 520 ms) than incongruent trials (IIM, 548 ms; CIM, 551 ms). The task × condition interaction was also significant [$F(3, 114) = 51.71$, $p < .001$], with RL in the spatial task being unaffected by condition and RL for congruent trials being faster than RL for incongruent trials in the digit task (see Fig. 1). The effect of local context served to modulate RL on congruent trials and had little effect on RL for incongruent trials in the digit task.

The digit task ($M = .10$) elicited more errors than the spatial task [$M = .08$; $F(1, 38) = 8.11$, $p < .007$]. The error data revealed a significant effect of condition [$F(3, 113) = 25.98$, $p < .001$], in which more errors are made on incongruent trials (II$M = .12$, CI$M = .13$) than congruent trials (CC$M = .06$, IC$M = .06$). Task and order

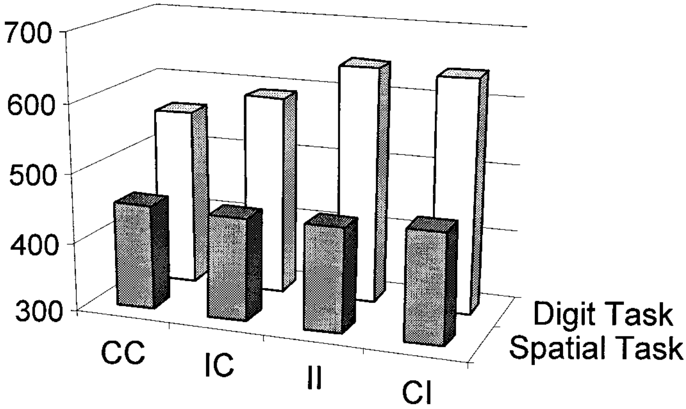

FIG. 1. Mean response latency for the digit identity and spatial location identification tasks for Experiment 1 as a function of local context. Note that response latency in the digit task is uniformly slower than in the space task, and that the effects of condition and local context are primarily reflected in the digit task.

interacted [$F(1, 38) = 14.358$, $p < .001$], such that error rates were equal in the two tasks when the digit task was performed first, but significantly lower when the spatial task was performed first.

Experiment 2. The RL data were analyzed in a 2 (proportion congruent) × 2 (condition) × 2 (order) ANOVA. As in Experiment 1, RL was faster for congruent ($M = 602$ ms) than incongruent [$M = 691$ ms; $F(1, 38) = 227.72$, $p < .001$] trials. More importantly, the proportion congruent × condition interaction was significant [$F(1, 38) = 86.96$, $p < .001$], with the interference effect of spatial location on digit identification being greater in the mostly congruent ($M = 133$ ms) than in the mostly incongruent ($M = 45$ ms) condition. Furthermore, this effect resulted from a significant modulation of RL for both the congruent (MC$M = 584$ ms, 95% CI ± 30 ms; MI$M = 620$ ms, 95% CI ± 33 ms) and the incongruent (MC$M = 717$ ms, 95% CI ± 38 ms, MI$M = 665$ ms, 95% CI ± 33 ms) trials.

Errors were more frequent in the MC condition ($M = .10$) than in the MI condition [$M = .08$; $F(1, 38) = 8.98$, $p < .005$] and for incongruent trials ($M = .14$) than congruent trials [$M = .04$; $F(1, 38) = 69.01$, $p < .001$], and these effects interacted [$F(1, 38) = 26.46$, $p < .001$], reflecting the greater number errors for incongruent trials in the MC ($M = .18$, 95% CI ± .04) than MI ($M = .11$, 95% CI ± .02) condition and the greater number of errors for congruent trials in the MI ($M = .05$, 95% CI ± .01) than MC ($M = .03$, 95% CI ± .01) condition.

Discussion

The findings from the present experiments reveal a pattern of data common to studies of the Stroop and Stroop-like tasks. One stimulus dimension (i.e., spatial location) was dominant over the other (i.e., numeric identity). Also, responses were faster and more accurate for congruent trials than incongruent trials and this effect was primarily expressed in the digit task. Local context served to modulate response latency for congruent trials in the digit task and had no effect on response latency for incongruent trials. The effect of global context was similar to that observed in other studies using the Stroop task, with the interference effect being attenuated when trials were mostly incongruent. Differences in the influence of local and global context on RL and accuracy lead to the suggestion that these effects may arise from the operation of separable attentional mechanisms. This is consistent with other data from our laboratory indicating that local context effects are expressed equally in older and younger adults, while older and younger adults are differentially influences by global context (West & Baylis, 1998).

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