Interference from Irrelevant Features on Visual Discrimination by Macaques (Macaca fuscata): A Behavioral Analogue of the Human Stroop Effect

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ABSTRACT

To study the operation of selective attention in a conflict situation with automatic processes, we trained four Japanese macaques extensively on a manual go/no-go task. The monkey had to discriminate either the color, shape, motion direction, or location of a visual stimulus. In each trial, the behavioral meaning of the relevant feature ("GO" or "NO-GO") could either be congruent or incongruent with irrelevant features of the same stimulus. Reaction times were slowed and error rates increased when irrelevant stimulus features were incongruent with the required response. The effects were obtained when the monkey attended to the color, shape, or motion direction, but not when it attended to the location of the stimulus. The effects were cumulative so that the interference from one incongruent feature was smaller than that from two incongruent features. We propose that the present paradigm provides a behavioral analog of the human Stroop effect.
Interference from Irrelevant Features on Visual Discrimination by Macaques:  
A Behavioral Analog of the Human Stroop Effect

Being able to attend to relevant visual information is a critical condition for success in a great variety of tasks as trivial as choosing the ripest berry or as life-threatening as crossing through a predator’s territory. Experimental psychologists investigate the individual’s ability to pay attention by examining patterns of costs and benefits to information processing in the visual field (for a comprehensive introduction, see LaBerge, 1995). This ability appears not only in humans but also in non-human animals that experience a complex visual world such as pigeons (D. S. Blough, 1993; Fremouw, Hermanson, & Shimp, 1998) or monkeys (Roberts, Robbins, & Everitt, 1988; Tomasello & Call, 1997).

To understand the properties of visual selective attention it is important to study its operation in a conflict situation when relevant information is embedded in an environment with competing irrelevant information (Van der Heijden, 1992). As such, the Stroop test (Stroop 1935/1992; Treisman & Fearnley, 1969) has led to a vast amount of knowledge on humans’ ability of visual selective attention (for review, see MacLeod, 1991). This test obtains a behavioral cost when relevant information of a stimulus appears in conflict with irrelevant information from the same
stimulus (Zhang & Kornblum, 1998). This behavioral cost, often termed Stroop effect, was found initially with a color-naming task. When normal human subjects are asked to name the color of a word, they respond more slowly and less accurately when the meaning of the word (e.g., “RED”) is incongruent with the color in which it is presented (e.g., green) than when meaning and color are congruent.

Current theory proposes that the Stroop effect is due, at least in part, to automatic processing of irrelevant information (Cohen, Dunbar, & McLelland 1990; Zhang, Zhang, & Kornblum, 1999). On this view, taking the original Stroop task as an example, word recognition occurs automatically and in parallel with color discrimination. As a result, both processes activate different color representations, leading to a competition between the required color representation (activated by selective attention to visual color) and the inappropriate color representation (activated by automatic word recognition).

At present, only one study has reported a Stroop-like effect with non-human animals (rhesus monkeys), using a relative-numerousness task with digits (Washburn, 1994). The study by Washburn showed one particular type of interference on attentional control, that is, from a local level of processing (the numeric identity of individual elements) on a global level of processing (the density or number of a group of elements). We investigated whether Stroop-like interference can also be obtained with different types of
attentional control, in tasks with relatively simple stimuli.

We devised a go/no-go paradigm with Japanese monkeys that were trained extensively to discriminate either the color, motion direction, spatial location or shape of a single visual target. Further, and more importantly, this multidimensional paradigm allowed us to test interference effects from multiple irrelevant features in concert. At present, models of Stroop-like interference remain silent concerning possible interaction among multiple irrelevant features. Yet such interaction could shed light on the structure of processing streams that lead to Stroop-like interference.

Method

Subjects. The subjects were four experimentally-naïve adult male Japanese macaques (Macaca fuscata), each with a body weight of between 9 and 11 kg, checked daily. The monkeys received free food (dry pellets) with small amounts of fresh fruit or vegetables in their home cages, and free water throughout the weekend. On weekdays they received a daily minimum of 250 ml liquid (orange juice during experimental sessions, and if necessary, additional water in the home cage to reach the minimum amount of liquid). The monkeys were cared for in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and the guidelines of the Animal Care and Use
Committees at the University of Tokyo and Juntendo University.

**Apparatus.** The experimental set-up consisted of a monkey chair in front of a 20 inch CRT (HC39PEX, Mitsubishi) placed at eye level at a distance of 90 cm in a sound-attenuated, dimly lit room. A lever consisting of a small plastic disk, 2.0 cm in diameter, was used for the manual responses. The lever was attached to the monkey chair in front of the right hand at the height of the elbow in such a way that the monkey could reach it with the right hand only. Personal computers (PC-386VE, Epson) were used to control the presentation of the stimuli on the CRT and to register manual responses.

**Behavioral task and stimuli.** The monkey was presented with a multidimensional visual stimulus, and had to discriminate one of its features to make a correct go or no-go response. The sequence of events in a trial was as follows. The monkey was required to press the lever to initiate a trial, and to keep holding down the lever. A fixation spot (0.3° in diameter) then appeared at the center of the display. Following a variable delay (1-2 s), the fixation spot dimmed and at the same time the target stimulus appeared in an unpredictable location at 4.1° from the fixation spot. The target was presented for 200 ms. The monkey had to release the lever within 0.8 s after target appearance in case of a go trial, or refrain from releasing the lever for at least 1.2 s after target appearance in case of a no-go trial. In a no-go trial the fixation spot became
bright again if the monkey continued to hold the lever throughout the 1.2 s dim period. Then, after the dim period, the monkey could release the lever at any time to obtain the reward. There was a 5 s inter-trial interval. If the monkey made an error, the same trial was repeated (i.e., a “correction trial”) after a prolonged inter-trial delay (3 s additional waiting period). These correction trials were used only as negative feedback, and were excluded from data analyses. Each correct response was rewarded with a drop of orange juice (0.25–0.3 cc).

The target stimulus consisted of moving colored dots presented in a limited area (with a maximal height and width of 6.2°) against a black background. This limited area functioned as a stationary presentation window through which the dots could be seen moving. Outside this window, the entire screen was black except for the fixation spot. All of approximately 280 dots (11% density) were of the same color and moved unidirectionally at 6°/s; apparent motion was produced by successive frame replacement (4 frames). The shape of the target stimulus was determined by the virtual contours of the stationary presentation window. Thus, the target stimulus appeared as a visual object in which four features could be distinguished: color of the dots inside the object, motion direction of the dots inside the object, location of the object, and shape of the object. We used two stimulus sets for each monkey, for instance, Set 1 with red/green color, leftward/ rightward motion, left/right
location, and circle/plus shape, and Set 2 with yellow/purple color, upward/downward motion, up/down location, and vertical bars/diamond shape.

The monkeys were required to discriminate one of the target features to make a correct go or no-go manual response. The behavioral meaning ("GO" or "NO-GO") of each target feature was fixed for each monkey during both training and testing, but could be either relevant or irrelevant depending on the attention condition. The color of the fixation spot indicated which of the target features the monkey should attend to. For instance, a yellow spot indicated that the monkey should attend to color, while a purple spot indicated that the monkey should attend to motion direction. Throughout blocks of 50 trials, the monkey had to attend to the same visual dimension (i.e., the color of the fixation spot remained constant). Daily, the monkey was presented with a maximum of 21 blocks. After each block, the color of the fixation spot was changed systemically so that the monkey performed an equal amount of trials in each attention condition.

The correct response to a particular multidimensional target depended on only the relevant stimulus feature, and so could vary across attention conditions. For instance, green could be associated with "GO" and leftward motion could be associated with "NO-GO", in which case the correct response to a green, leftward moving target would be "GO" in the color condition but "NO-GO" in the motion condition. With this
design, then, in each trial irrelevant stimulus information could be either congruent or incongruent with the required response (see Figure 1, top panel).

**Training and probe test.** The monkeys were trained extensively (during 6 to 8 months with daily sessions of about 1,000 trials) on the go/no-go task in different attention conditions. In the first stage, each association between a stimulus feature and its behavioral meaning was trained in isolation so that the monkeys could learn the association as soon as possible. For instance, to facilitate learning that the color green was associated with the go response and the color red with the no-go response we trained the monkey using green and red stimuli with neutral irrelevant features (without apparent motion, with a square shape, and presented at the center of the display). Training on separate features was continued up to more than 30,000 trials, that is, we “over-trained” the monkeys. In the second stage, the monkeys were trained with different combinations of features. Three monkeys were trained in three attention conditions: one in the shape, color, and motion conditions; the other two in the location, color, and motion conditions. One monkey was trained in two attention conditions: the color and motion conditions.

When training was completed, we checked with a probe test whether the monkeys had learned to attend to each relevant stimulus feature. In this test, the monkeys were presented with new stimuli on 10% of the trials during
sessions on three consecutive days. All other aspects of the behavioral task were kept the same as during regular training and experimental sessions. To create new stimuli, we recombined individual features from stimulus sets 1 and 2. Each of the four monkeys performed significantly better than chance level on the probe trials in all attention conditions, with error rates generally below 10%, indicating that the monkeys relied on the meaning of the relevant features to select the required manual response (go or no-go).

After the probe test, we proceeded to the experimental sessions on consecutive days during a four- to eight-day period depending on the number of attention conditions. The monkeys were tested in each attention condition with more than 600 trials for each stimulus set. Analyses were performed on reaction time (RT) for correct responses in go trials, and on error rates in both go and no-go trials. RTs more than two standard deviations from the mean RT in a condition were eliminated. RTs from no-go trials were not analyzed because the monkeys were required to make fast responses only in go trials.

Results

Stroop-like effects were obtained in all four monkeys, as indicated by slower responses in go trials and by higher error rates in both go and no-go trials when irrelevant
information was incongruent with the required response compared to when it was congruent.

The monkey in two attention conditions. For the monkey trained in two attention conditions, we present the cumulative frequency distributions of RTs in the color condition (Figure 1, middle panel) and in the motion condition (Figure 1, bottom panel), data collapsed across the two stimulus sets. The shapes of the distributions are representative for the results with the other monkeys. The distributions of RTs appear to be uni-modal, with similar shapes for congruent and incongruent trials, indicating that Stroop-like interference occurs in almost the entire range of observations, not just in the tail of the distribution.

We computed two-tailed paired t tests to compare statistically between congruent and incongruent trials, based on mean data from each block of trials. In the color condition, RTs on incongruent trials were 15 ms slower than on congruent trials (446 vs 431 ms), \( t(19) = 16.88, p < .01 \). In the motion condition, RTs on incongruent trials were 21 ms slower than on congruent trials (468 vs 447 ms), \( t(21) = 19.64, p < .01 \). On error rates, collapsed across go and no-go trials, the Stroop-like effects were 4.3 % (9.4 on incongruent trials vs 5.1 % on congruent trials) in the color condition, \( t(19) = 7.51, p < .01 \), and 10.3 % (13.5 on incongruent trials vs 3.2 % on congruent trials) in the motion condition, \( t(21) = 9.34, p < .01 \).
Overall analysis for the monkeys in three attention conditions. With the monkeys that were trained in three attention conditions, overall, we obtained 20 ms slower RTs in go trials and 4.1% higher error rates across go and no-go trials when all irrelevant information was incongruent as compared to when it was congruent with the required response. Figure 2 presents mean RTs in go trials and error rates collapsed across go and no-go trials separately for the color (top left), motion (top right), location (bottom left), and shape (bottom right) conditions.

For the overall analysis, we used a repeated measures analysis of variance (ANOVA), Monkeys x Congruency, with Monkeys as between-subjects factor and Congruency as within-subjects factor. For this analysis, we used mean data from each stimulus set in each attention condition (and so each monkey contributed six data points). In this analysis, any variance from stimulus set or attention condition would contribute to the error variance. The effect of Congruency on RT was statistically reliable, $F(2, 30) = 15.48$, $MSE = 116.35$, $p < .01$. Also the between-subjects factor Monkeys produced a significant effect on RT, $F(2, 15) = 17.36$, $MSE = 1282.57$, $p < .01$; however, there was no interaction between the between-subjects factor Monkeys and Congruency, $F(4, 30) = 2.07$, $MSE = 116.35$, $p > .1$. RTs were faster when all irrelevant features were congruent (366 ms) than when one irrelevant feature was incongruent (373 ms). RTs were the slowest when all irrelevant features were incongruent (386
ms). Post-hoc Tukey HSD tests showed that all contrasts between levels of Congruency (all-congruent, heterogeneous, or all-incongruent irrelevant features) were significant ($p < .01$).

For error rates, a repeated measures ANOVA, using one additional within-subjects factor (Go/no-go response), showed a significant main effect of Congruency, $F(2, 30) = 7.46$, $MSE = .0022$, $p < .01$. Error rates tended to be lower on go trials (3.2 %) than on no-go trials (7.3 %), $F(1, 15) = 3.25$, $MSE = .0139$, $p < .1$. Neither the factor Monkeys nor any of the interactions reached statistical significance, all $F$’s < 2. Error rates were lower when all irrelevant features were congruent (3.5 %) than when one irrelevant feature was incongruent (4.8 %). Error rates were largest when all irrelevant features were incongruent (7.6 %). Post-hoc Tukey HSD tests showed that all contrasts between levels of Congruency were significant ($p < .05$).

Tests of super-additivity. To evaluate further whether the effects of the three levels of Congruency were super-additive, we performed a repeated measures ANOVA (Monkeys x Congruency) on the differences of one minus no incongruent features against the differences of two minus one incongruent features. There was a main effect of Congruency, $F(1, 15) = 6.05$, $MSE = 50.58$, $p < .05$, indicating that the average difference of one minus no incongruent features ($373 - 366 = 7$ ms) was smaller than that of two minus one incongruent features ($386 - 373 = 13$ ms). Put differently, two
incongruent features created a larger disturbance than twice the effect from a single irrelevant feature. No other effects reached statistical significance.

As with RTs, the repeated measures ANOVA (Monkeys x Congruency x Go/no-go response) comparing differences between error rates showed that the effects from two incongruent features were super-additive $F(1, 15) = 6.64$, $\text{MSE} = .0004$, $p < .05$. No other effects reached statistical significance.

Separate analyses for each attention condition.
Comparing between attention conditions, RT was the fastest in the location condition (346 ms), followed by the color condition (370 ms), and with the slowest RTs in the motion and shape conditions (391 ms and 399 ms, respectively).
Because the overall analysis showed a main effect of the between-subjects factor Monkeys, we evaluate the Stroop-like effects as a function of attention condition separately for each monkey. We used repeated measures ANOVA’s on RT and error rates for each monkey in each attention condition, with Congruency as within-subjects factor, using mean data from each block of trials. The effects of Congruency were significant for both dependent measures in all cases except when the monkeys had to attend to the target’s location ($p > .05$). These results can be seen in Figure 2 as the bars for RTs and error rates clearly change in size as a function of congruency in all attention conditions except in the location condition.
Post-hoc Tukey HSD tests on the data from the two monkeys trained on the location condition showed that both in the color and motion conditions all contrasts between levels of Congruency were significant, \( p < .05 \). These results indicate that location information as an irrelevant feature did interfere with attentional processing. Averaging across the two monkeys, Stroop-like interference from the location feature (comparing incongruent-location trials versus congruent-location trials, collapsing across the other irrelevant feature) were 7 ms in the color condition and 12 ms in the motion condition.

Discussion

Four Japanese macaques were trained on a go/no-go task based on visual feature discrimination. The manual responses of all four monkeys were disturbed, as in the original experiment by Stroop (1935/1992), when irrelevant information appeared in conflict with the required response. The effects were obtained in the color, motion, and shape conditions, but not in the location condition. Further, the effects from multiple irrelevant features were super-additive, so that the interference from two incongruent irrelevant features was more than twice as large as that from only one incongruent feature.

These results were obtained while the monkeys gave clear evidence of using selective attention to perform the task.
Error rates were generally below 10%. In addition, overall RTs were different in the four attention conditions, indicating that the monkeys were relying their decisions on different types of processing in each attention condition. The results of the probe test further showed that the monkeys had learned to attend to the relevant stimulus features, even with novel targets. Yet, in spite of the clear use of selective attention, the monkeys were unable to prevent irrelevant information from intruding on their decision making. These results, therefore, are Stroop-like as they show influences from the meaning of irrelevant stimulus features on the operation of selective attention, presumably because the irrelevant stimulus features were processed automatically (Cohen et al., 1990; Zhang et al., 1999).

Our present data could be said to depart from the original Stroop effect inasmuch as we found interference from irrelevant features to work in reciprocal directions. This result at first may seem to be at odds with the original Stroop effect that works only in one direction, from a color word on a visual color. The absence of a reverse Stroop effect from a visual color on a color word, however, can be explained in terms of “strength of association” (Logan, 1980; MacLeod, 1991). On this view, the amount of practice determines the size of the Stroop effect. MacLeod and Dunbar (1988), for instance, showed that Stroop-like interference can work in reciprocal directions in shape- and color-naming tasks with novel objects for which participants have to use
color names. Similarly, the monkeys in the present study had been trained to an equal extent in different attention conditions. Our data with effects in reciprocal directions, therefore, are consistent with the role of practice in the generation of Stroop-like interference.

Comparing the original Stroop task with the present discrimination tasks, one might object that in our paradigm the relevant and irrelevant stimulus features are equally compatible with the response modality. Indeed, in the original Stroop effect, a fraction of the interference seems to be due to the fact that an irrelevant word is compatible with the response modality (speech production), while the relevant visual color is not. Stroop-like interference, however, does still occur even when stimulus-response compatibility is kept constant (MacLeod, 1991). For instance, irrelevant color words also produce interference when participants are asked to respond manually to visual colors (e.g., Logan, Zbrodoff, & Williamson, 1984; Virzi & Egeth, 1985).

Although we observed Stroop-like interference in all four monkeys and both with RTs and error rates, there were some differences in the size of the Stroop-like effects according to the attention condition. Most notably, we could not find clear Stroop-like interference in the location condition. Both monkeys that were trained to discriminate location, were insensitive to irrelevant information in the location condition. When location information was irrelevant,
on the other hand, we did observe Stroop-like interference from the location of the target on color and on motion processing. We propose that the entire pattern of data with location features can be explained by the spatial extent of information processing.

On this view, the monkeys may be able to discriminate the location of the target already during a preliminary, coarse analysis of the global image, while the discrimination of other visual features of the target requires a more locally focused analysis, concentrated on the region of space occupied by the target (Müller & Rabbit, 1989). Consequently, only responses in the location condition can be generated at the global level without interference from other visual features at the local level. Irrelevant location information, on the other hand, can still interfere with a more locally focused analysis of the image, assuming that the global level of analysis precedes the local level (e.g., Lamb & Robertson, 1990).

Our present data, collected with monkeys that were trained on three types of discrimination, also are the first to show cumulative effects from two irrelevant features. Both with RT and error rates, performance was disturbed more than twice as much if two irrelevant features were incongruent with the required response than if only one irrelevant feature was incongruent with the required response. In other words, two incongruent features created a non-linear or super-additive disturbance effect. Such super-additivity from
multiple irrelevant features had not yet been observed because previous studies with humans invariably compared only two types of processing.

The super-additive disturbance effect is important for several reasons. First, the effect suggests that the observed Stroop-like interference is governed by negative interference or inhibition rather than by facilitation. To make this clear, let us take the heterogeneous case with one congruent and one incongruent feature as the reference level. Judging by this reference level, the replacement of a congruent by an incongruent irrelevant feature (i.e., an increased possibility of negative interference) leads to a stronger effect than the opposite case, the replacement of an incongruent by a congruent irrelevant feature (i.e., an increased possibility of facilitation). This finding is consistent with observations of stronger inhibition than facilitation effects in previous studies that have used baseline or “neutral” trials to tease apart the two types of processes in Stroop-like interference (e.g., Washburn, 1994).

Further, the super-additive disturbance effect suggests that the automatic processes generated by different features of the same stimulus become integrated, or reinforce each other at a stage of information processing prior to the execution of the behavioral response. Thus, the super-additive effect already puts some constraints on explanations of Stroop-like interference, favoring explanations that incorporate non-linear processes in the organization of
information-processing streams. As such an explanation for the present multidimensional paradigm, we propose that multiple irrelevant features can project onto the same incongruent internal representation (e.g., a “NO-GO” representation during a go trial). In terms of cognitive modeling (e.g., Zhang & Kornblum, 1998), the input from a single irrelevant feature may sometimes not suffice to activate a specific incongruent internal (cognitive) representation. Such a representation, however, might be pushed above its threshold for activation by the combined input from two irrelevant features, thus producing superadditive effects.

In sum, the present results demonstrate that the go/no-go visual discrimination task with monkeys provides a valid animal model to extend our understanding of the human Stroop effect. The go/no-go visual discrimination already proved to be useful for neurophysiological investigation (Sakagami & Niki, 1994a,b; Sakagami & Tsutsui, 1999). The present data show that the paradigm can also be employed for studying the neural correlates of interference from automatic processes on the operation of selective attention.
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AUTHOR NOTE

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FIGURE LEGENDS

Figure 1. Schematic illustration of the experimental design (top panel); cumulative relative frequency distributions of the RTs of the monkey that was trained in two attention conditions (middle and bottom panel). The top panel shows one color and one motion direction associated with the go response (“GO”), while the alternative color and motion direction are associated with the no-go response (“NG”). (The actual stimuli had different colors and random dot motion.) The same stimuli were used in both attention conditions, and so the irrelevant stimulus feature could be either congruent or incongruent with the required response. The cumulative frequency distributions of the RTs are based on data from go trials only and are presented as a function of congruency during discrimination of color (middle panel) and motion direction (bottom panel). The data from congruent trials are presented in black; those from incongruent trials in gray. In both attention conditions, a Stroop-like effect was present across almost the entire range of observations.

Figure 2. Mean RTs and error rates of the monkeys that were trained in three attention conditions. The data are presented as a function of congruency of the irrelevant features with the required response (“Co / Co” means that both irrelevant features were congruent; “Co / In” means that one irrelevant feature was congruent, the other incongruent;...
“In / In” means that both irrelevant features were incongruent). The data are presented separately for the color (top left), motion (top right), location (down left), and shape condition (bottom left); mean RTs above error rates. The mean RTs are based on go trials only; the error rates are collapsed across go and no-go trials.
Stroop-like Interference in Monkeys

- **Attention to**
  - Color: GO, NG, GO, NG
  - Motion: GO, GO, NG, NG

**COLOR**

- Congruent
- Incongruent

**MOTION**

- Congruent
- Incongruent