

Global and local processing of visual patterns in macaque monkeys

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Human subjects generally perceive the global form of hierarchically organized visual patterns faster than the local form. To test whether macaque monkeys show a similar precedence for global processing, two monkeys were trained to discriminate either the global or local form of hierarchical visual patterns. The response time to discriminate the global form was shorter than that to discriminate the local form. Consistent patterns, in which the global and local forms were identical, were discriminated faster than inconsistent ones, in which the two

forms were different from each other, both in discrimination of the global form and of the local form. Similar results were obtained in two human subjects who were subjected to the identical tests. The results suggest that, both in monkeys and humans, the global form is processed faster than the local form with a temporal overlap which allows bidirectional interactions between the two processes. *NeuroReport* 11:2881–2884 © 2000 Lippincott Williams & Wilkins.

Key words: Global and local processing; Global precedence hypothesis; Hierarchical visual patterns; Macaque monkeys; Visual discrimination; Visual attention

INTRODUCTION

On the basis of psychological experiments in human subjects, Navon proposed the global-precedence hypothesis which states that perception of the global form of hierarchically organized visual patterns (large letters made of small letters) precedes perception of the local form [1]. Two results in his experiments support the hypothesis. First, the response time to identify the global form was shorter than that to identify the local form (global advantage). Second, the global form influenced the speed of processing of the local form, but not *vice versa* (global to local interference). When subjects identified the local form, the response time to consistent patterns (e.g., large X made of small Xs) was shorter than that to inconsistent ones (e.g., large Y made of small Xs). This difference between the response times of subjects to consistent and inconsistent patterns was not observed in identifying the global form.

To our knowledge, only one study addressed the issue whether the global-precedence hypothesis holds for non-human primates. Fagot and Deruelle reported that, in contrast to human subjects, baboons exhibit a shorter response time in discrimination of local forms rather than of global forms [2]. This raised a question of whether the faster processing of global form is universal among primates or specific to humans. To further pursue this issue, two macaque monkeys were trained to discriminate either the global or local form of hierarchical visual patterns. We chose macaque monkeys, whose visual system has been

the most intensively studied among all primates including humans [3,4], as subjects. Two human subjects also received identical behavioral tests for comparison between the two species.

MATERIALS AND METHODS

Two male macaque monkeys (*Macaca fuscata*), MKT and SNAT, were used in the present experiment. A head holder was attached to the top of the monkey's skull to fix their head to a monkey chair. The surgery was performed under aseptic conditions, and an antibiotic (piperacillin sodium, 30 mg/kg, i.m.) and an analgesic (ketoprofen, 0.5 mg/kg, i.m.) were injected for a few weeks after the surgery. All experiments were conducted in accordance with the Guide for the Care and Use of Laboratory Animals (1996) from the National Institutes of Health.

Visual stimuli were in the form of hierarchically organized letters made of small letters (Fig. 1). In each trial, a visual stimulus was presented for 100 ms at the center of a liquid crystal display using a computer. We measured the monkeys' eye movements using an infrared CCD camera system (X-Y tracker C3162, Hamamatsu Photonics K.K.) and verified that their gaze was maintained within 1° of the center of the visual stimulus during the stimulus presentation. To instruct the monkeys in the timing of visual presentation and response, a small point (0.2 × 0.2° square) was presented for 500 ms before the stimulus onset and for 600 ms after the stimulus offset. In global (or local)

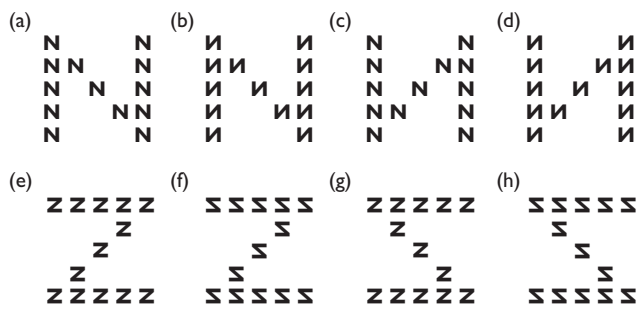


Fig. 1. Visual stimuli used in the present experiment. The global and local forms of hierarchical visual patterns were N, Z, reversed N or reversed Z. A large letter (2.7°) was constructed using a 5×5 matrix of small letters (0.4°), each separated by a distance of a half letter. In the global task, the patterns **a**, **b**, **e** and **f** were assigned to go responses, and the patterns **c**, **d**, **g** and **h** were assigned to no-go responses. In the local task, the patterns **a**, **c**, **e** and **g** were assigned to go responses, and the patterns **b**, **d**, **f** and **h** were assigned to no-go responses. The visual patterns were white (210 cd/m^2) on a black background (5.2 cd/m^2) on a liquid crystal display.

tasks, they were required to discriminate the global (or local) form of visual patterns. When a target (N or Z) appeared at the global (or local) level in a global (or local) task, they were trained to push a lever down with their right hand within 500 ms after the disappearance of the visual stimulus (go response). When a distracter (reversed N or reversed Z) appeared at the attended level, they had to wait until the small point was turned off and then push the lever down (no-go response). The monkeys were rewarded for their correct responses by a drop of water or juice. A block of 80 trials consisted of 40 go response trials and 40 no-go response trials arranged in a pseudorandom order. The level at which the target appeared was kept constant throughout a block of trials. As no instruction was given to direct attention to either the global or local level, the monkeys had to find out by trial and error which of the tasks, global or local, they were performing. Only one or two blocks of trials was usually needed to shift between the two tasks to reach a performance rate of $>90\%$ correct responses.

Behavioral data were obtained from test sessions for 7 days after the monkeys reached a performance rate of $>90\%$ correct responses. The error rate and the response time of go responses were analyzed in each subject by a two-way ANOVA, with globality (global task or local task) and consistency (consistent patterns or inconsistent patterns) as the main effects.

Two human subjects (HT and KS) were also tested for the same behavioral tasks to compare behavioral scores with those of the monkeys. Subject HT was one of the authors, and subject KS was naive to the experiment. After verbal instruction, a few warm-up trials were given to the human subjects, which was enough for them to reach a performance rate of $>90\%$ correct responses. The behavioral tests were performed for 2 days, and the mean behavioral scores were obtained over six blocks, each comprising 80 trials. The subjects were asked to fixate on a small point during trials. Other aspects of the experimental procedure were identical to those used in the monkeys. The test of human subjects using visual patterns identical to those

used for the monkeys is important for comparison, because the relative difference in the response time for discriminating global and local forms is affected by various factors of visual patterns, such as the overall size of visual stimuli and the retinal location of stimulus presentation [5–9] (for reviews see [10,11]).

RESULTS

Behavioral data obtained from the monkeys and the human subjects are summarized in Fig. 2. The monkeys were well trained for both global and local tasks, and they made only a few error responses in the test sessions (mean error rate: MKT, 5%; SNAT, 3%). The mean error rates for consistent patterns were lower than those for inconsistent patterns both in the global and local tasks (main effect of consistency: MKT, $F(1,24) = 25.27$, $p < 0.0001$; SNAT, $F(1,24) = 29.88$, $p < 0.0001$). In monkey SNAT, the mean error rates in the global task were lower than those in the local task (main effect of globality, $F(1,24) = 29.88$, $p < 0.0001$), and most error responses occurred for inconsistent patterns in the local tasks (globality \times consistency interaction, $F(1,24) = 22.51$, $p < 0.0001$). In monkey MKT, there was neither significant main effect of globality nor significant globality \times consistency interaction. In the two human subjects, the mean error rates were remarkably low in spite of only having a few warm-up trials (mean error rate: HT, 1%; KS, 1%). No difference between stimulus categories was found in the two human subjects.

The response time was shorter in global tasks than in local tasks for the two monkeys (main effect of globality: MKT, $F(1,24) = 19.45$, $p < 0.0005$; SNAT, $F(1,24) = 9.50$, $p < 0.01$). The response time to consistent patterns was shorter than that to inconsistent ones both in global and local tasks (main effect of consistency: MKT, $F(1,24) = 8.60$, $p < 0.01$; SNAT, $F(1,24) = 34.98$, $p < 0.0001$). Thus, interference between global and local processing occurred in both directions, i.e., global to local and local to global directions. The shorter response time was obtained with a lower error rate, indicating that the difference in response times was not explained by a trade-off between the error rate and the response time.

As in the monkeys, the response time of the human subjects in global tasks was shorter than that in local tasks (main effect of globality: HT, $F(1,20) = 16.34$, $p < 0.001$; KS, $F(1,20) = 11.09$, $p < 0.005$), and the response time was shorter for consistent patterns than for inconsistent ones in both global and local tasks (main effect of consistency: HT, $F(1,20) = 9.84$, $p < 0.01$; KS, $F(1,20) = 24.44$, $p < 0.0001$). The globality \times consistency interaction was significant only in human subject KS ($F(1,24) = 4.54$, $p < 0.05$).

The response time in the human subjects was longer than that in the monkeys by 70–140 ms (mean response time: MKT, 360 ms; SNAT, 352 ms; HT, 428 ms; KS, 496 ms). To compare the degree of global advantage and consistency effect between the monkeys and the human subjects, we calculated the relative differences of the mean response times between different task conditions for each subject (Table 1). The degrees of global advantage were in a similar range among all the subjects, although the global advantage of inconsistent patterns in human subject HT was larger than that of consistent patterns in monkey SNAT and human subject KS (multiple comparisons,

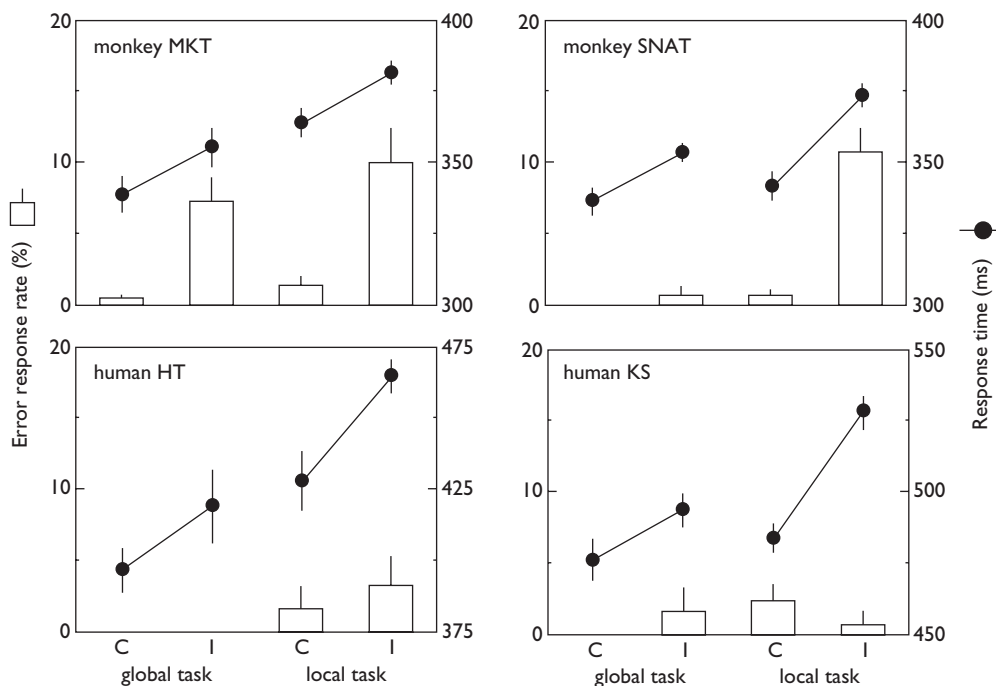


Fig. 2. Mean error rate and response time measured over 7 days in monkeys and six blocks in human subjects. Both error rates and response times were summarized for each task condition. Each bar represents s.e. Note that the scale for response time on the ordinate differs among the graphs. C: consistent patterns; I: inconsistent patterns. See text for more details.

Table 1. Mean (\pm s.e.) global advantage and consistency effect in monkeys and humans

		Monkeys		Humans	
		MKT	SNAT	HT	KS
Global advantage (ms)	Consistent	26 \pm 6	5 \pm 6	32 \pm 12	8 \pm 11
	Inconsistent	26 \pm 8	21 \pm 3	46 \pm 11	35 \pm 6
Consistency effect (ms)	Global task	17 \pm 3	17 \pm 3	23 \pm 15	18 \pm 5
	Local task	18 \pm 2	32 \pm 2	37 \pm 11	45 \pm 7

Global advantage: (response time in local task)–(response time in global task). Consistency effect: (response time to inconsistent patterns)–(response time to consistent patterns).

$p < 0.05$). There was no significant difference in the consistency effects among all monkeys and human subjects.

DISCUSSION

The response time was shorter in global tasks than in local tasks in both the monkeys and human subjects. The results suggest that the global form of hierarchical visual patterns was perceived faster than the local form in both species. In contrast, Fagot and Deruelle reported that baboons responded faster to local targets than to global targets in a task where human subjects showed global advantage [2]. Based on this result, they concluded that the global precedence is not universal among human and non-human primates. The correct response rate of baboons in their six experiments was significantly lower (53–74%; chance level 50%) than that of macaque monkeys (95–97%) in our experiment. In most experiments, the correct response rate was higher in the local tasks (61.7–89.2%) than in the

global tasks (50.4–70.2%), which the authors took as evidence supporting a local advantage [2]. The low correct response rate of the baboons in the global tasks, however, raises a concern that the baboons did not understand the framework of the task very well; they might attend first to the local targets even in the global task trials, thus the response time to the global form became longer than that to the local form.

In both global and local tasks, the response time of the monkeys and human subjects to consistent patterns was shorter than that to inconsistent ones. This was in contrast to Navon’s original report where his subjects showed a consistency effect only in global tasks [1]. Navon regarded the result as evidence for perceptive precedence for global forms [1]. This study showed that the consistency effect is not limited to the global to local direction, but can occur in the local to global direction as well. The results suggest that processing of the global form and the local form have

a temporal overlap which allows interaction between the two processes in either direction, although the global form is processed faster than local form as evidenced by the shorter response time in global tasks than in local tasks.

The mean response time was longer in the human subjects than in the monkeys by 70–140 ms. Although we do not know the exact cause of the difference in the response time between the two species, it might be partially attributable to the extensive training for the behavioral tasks in the monkeys. Despite the absolute difference in the response time, the amount of global advantages and consistency effects was similar in the monkeys and human subjects, suggesting a similarity of the visual mechanisms between the two species.

There is some evidence that different parts of the brain in humans and monkeys are preferentially involved in global or local processing. Neuropsychological and brain imaging studies in human subjects have suggested that the right and left hemispheres are involved in global and local processing, respectively [12–17]. However, these studies have not been able to specify particular brain areas consistently involved in either the global or local processing. In monkeys, inactivation by bilateral cooling of the dorsal part of the anterior inferior temporal cortex (IT) impaired discrimination of local processing, but not global processing [18]. No brain region in monkeys has so far been specifically implicated in global processing. In our ongoing study, we have applied positron emission tomography techniques to macaque monkeys to identify brain regions involved in global and local processing. The experiments provided evidence that the anterior part of the IT was more active under local trial conditions than under global ones, whereas the posterior part of the IT was more active under global trial conditions than under local conditions [19].

CONCLUSION

In both macaque monkeys and human subjects, the global form of hierarchical visual patterns was discriminated

faster than the local form, and consistent patterns were discriminated faster than inconsistent ones both in discrimination of the global form and of the local form. The amount of global advantages and consistency effects was nearly identical between the monkeys and human subjects in spite of the absolute difference of the mean response time of 70–140 ms. The results suggest that, both in monkeys and humans, the global form is processed faster than the local form with a temporal overlap, which allows interactions between the two processes in both global to local and local to global directions. It seems likely that a similar neural mechanism underlies the global precedence effect in macaque monkeys and humans.

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