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ORIGINAL PAPER

Effects of tilted orientations and face-like configurations on visual search asymmetry in macaques

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Abstract Visual search asymmetry has been used as an important tool for exploring cognitive mechanisms in humans. Here, we examined visual search asymmetry in two macaques toward two types of stimulus: the orientation of line stimuli and face-like stimuli. In the experiment, the monkeys were required to detect an odd target among numerous uniform distracters. The monkeys detected a tilted-lines target among horizontal- or vertical-lined distracters significantly faster than a horizontal- or vertical-lined target among tilted-lined distracters, regardless of the display size. However, unlike the situation in which inverted-face stimuli were introduced as distracters, this effect was diminished if upright-face stimuli were used as distracters. Additionally, monkeys detected an upright-face target among inverted-face distracters significantly faster than an inverted-face target among upright-face distracters, regardless of the display size. These results demonstrate that macaques can search a target efficiently to detect both tilted lines among non-tilted lines and upright faces among inverted faces. This clarifies that there are several types of visual search asymmetry in macaques.

Keywords Face · Visual search · Search asymmetry · Search efficiency · Macaque monkey

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Introduction

In a visual search task, an observer searches for a target item among numerous distracter items. The phenomenon in which the visual search produces different results when the target and distracter items are reversed (e.g., searching for a target item "A" among distracter items "B" relative to searching for a target item "B" among distracter items "A") is described as a visual search asymmetry. For example, we can detect a tilted line among vertical lines (Treisman and Gormican 1988; Foster and Ward 1991), an object in motion among stationary objects (Royden et al. 2001), or a particular colored (e.g., red) object among other particular colored (e.g., orange) objects (Treisman and Gormican 1988) more easily than the opposite configurations. The basic feature processed pre-attentively plays a key role in the efficient search. A previous study (Wolfe et al. 1992) argued that the orientation of an object is categorized pre-attentively as four types of tilt information (basic features) that are processed in parallel. Therefore, searching for a tilted item (which holds tilt information) among vertical items (which lacks tilt information) is easier than vice versa. Likewise, searching for an object with a particular additional feature among objects with no such feature is easier than vice versa.

Following a classic study by Treisman and Gelade (1980), visual search asymmetries have been used in many human studies as an important tool for exploring cognitive mechanisms, particularly in relation to visual attention or visual search itself (Wolfe 2001). However, few studies have been conducted concerning search asymmetry in animals. Allan and Blough (1989) tried to investigate search asymmetry in pigeons using a simple line form (e.g., a circle or triangle) and the form created by adding a feature (a line or a gap) to that form for either the target or the distracter stimulus.

However, the pigeons failed to show search asymmetry. Pearce and George (2003) also investigated search asymmetry in pigeons. When the target held more distinctive features (color cues) than the distracters (e.g., the target patterns were groups of both red and blue color dots, while the distracter patterns were groups of blue color dots only), the pigeons' accuracy was significantly greater than vice versa. Pearce and George argued that the experiments provided a novel demonstration of visual search asymmetry in pigeons. Search asymmetry has also been investigated in chimpanzees by conducting a visual search task using several sets of geometric forms (Tomonaga 1993). When a stimulus containing plural features was shown as the target and stimuli with a single feature as the distracters, the chimpanzees found the target more quickly, irrespective of the display size. They also efficiently searched for a moving target among stationary distracters (Matsuno and Tomonaga 2006).

Overall, while chimpanzees clearly demonstrate asymmetry in visual search tasks similar to that observed in humans, the status of search asymmetry in pigeons remains unclear. Search asymmetry in non-human animals has only been studied for these two species till date. To confirm that the phenomenon of search asymmetry is observed not only in humans and chimpanzees but also in many other species, additional investigation of other non-human animals is required. In particular, it is important to investigate whether search asymmetry is exhibited in other non-human primates such as old world monkeys, which occupy an evolutionary position between chimpanzees and pigeons. It is more likely that old world monkeys show search asymmetry than pigeons because results that partially support this possibility have been previously reported. For example, monkeys showed faster detection of deviant pictures of snakes than that of flowers; however, the study did not investigate whether this was attributable to search efficiency or asymmetry (Sibasaki and Kawai 2009).

Let us now consider another type of visual search asymmetry: asymmetry of the face. The face consists of more features and is relatively complicated than other simple forms that are frequently experienced visually (e.g., lines, colors, motions); moreover, the face contains social signals. Thus, face is a rich visual resource that can be recognized at a glance. Many studies have reported that humans show search asymmetry of the face. For example, there is an efficient search for faces of one's own race (Levin 1996; Levin and Angelone 2001), faces displaying the emotion of anger (Hansen and Hansen 1988; Horstman and Bauland 2006), one's own face (Tong and Nakayama 1999), and visually familiar faces (Montoute and Tiberghein 2001). Some studies have argued that the face is processed pre-attentively for basic features (Lewis and Edmonds 2005; Hershler and Hochstein 2005). However, visual search asymmetry of the face is sometimes considered to reflect processing in a serial manner, following the pre-attentive process (Wolfe 2001; Nothdurft 1993).

In a comparative cognitive study of the visual search task for faces, Tomonaga (2007) demonstrated search asymmetry for facial orientation in chimpanzees. Both real human faces and caricatures of human faces were detected faster when an upright-oriented face was defined as the target and inverted oriented faces were defined as distracters than when the target and distracters were reversed. These results were not seen when non-face-like objects or dogs' faces were used. It seems reasonable to conclude that this study shows face-specific upright superiority for chimpanzees in the visual search task even though it is unclear whether a parallel search strategy was used in the detection of the upright face. In addition, Tomonaga and Imura (2010) showed that chimpanzees more efficiently detect a human face with direct gaze among faces with averted gazes than vice versa.

Overall, these studies strongly suggest that humans and chimpanzees process faces in a similar manner. However, it must be noted that there is limited evidence from animal studies to show visual search asymmetry of the face. Although numerous experiments in old world monkeys have partly supported their face recognition abilities (behavioral studies: Keating and Keating 1993; Parr et al. 1999; Parr and Hecht 2011; Gothard et al. 2009; Martin-Malivel et al. 2006; Dahl et al. 2009; Adachi et al. 2009; neuroscience studies: Bruce et al. 1981; Perrett et al. 1982; Tsao et al. 2003; Eifuku et al. 2004, 2010; De Souza et al. 2005; Sugase et al. 1999), no study has yet explored their efficiency of visual search for faces. If such search asymmetry is confirmed in these monkeys with rich face recognition abilities, there will be good evidence to show that the processing related to visual search asymmetry of the face can be shared by different species, in parallel with face recognition abilities. On the contrary, if visual search asymmetry is not confirmed in these animals in spite of their rich abilities, this may be attributable to differences in the processing of visual search. That is, a study exploring the efficiency of visual search for faces in the macaque will provide an important basis for understanding the relation between visual search asymmetry of the face and face recognition itself.

The present study examined search asymmetry in macaques, a type of old world monkey. The first experiment examined search asymmetry between different orientations of line objects, and the following experiments investigated differences in search efficiency between face orientations. As mentioned above, chimpanzees showed face-specific upright superiority, and many studies in humans have reported that an inverted face disrupts the face recognition seen with upright faces (Maurer et al. 2002). Because macaques also show a bias toward a particular orientation of the face (Tomonaga 1994; Parr et al. 2008), if the superiority for that orientation of the face is also present in the visual search task, it is likely that the particular face orientation can work as a strong distracter in the search for a tilted line. Therefore, the second experiment examined the effect of face orientation presented as a distracter stimulus in the search for a tilted or a horizontal line. The third experiment examined the search asymmetry of the face using particular orientations. If monkeys show search efficiency toward the face, it will provide a good evidence to support the existence of these abilities in this species. The last experiment examined differences in the search asymmetry between faces and non-face objects that have similar global shapes, in order to confirm the effect of face configurations in visual search.

Methods

Subjects

Two Japanese monkeys (*Macaca fuscata*, one male and one female, age: 3–4 years, weight: 4.5–6.5 kg) were used for the experiment. The monkeys were housed alone, one per cage, but they were allowed visual and auditory communication with monkeys housed in other cages within the same room. Their interaction was also limited to a few human caretakers, each of whom wore a facemask and protective clothing. Neither of the subjects had prior experience of any experimental task. All experimental protocols used in the study were approved by the Animal Care and Use Committee of University of Toyama (Permit # MED-46); the protocols also conformed to the National Institutes of Health guidelines for the humane care and use of laboratory animals, and the ARVO statement for use of animals in ophthalmic and vision research.

Stimuli

Six gray-scale images were used as stimuli, each of which comprised a circular outline containing some inner circles on a black background (70 × 70 pixels, 2.0° of visual angle) (Fig. 1). The inner components of the basic image comprised a row of three circles of the same size. In experiment 1, we used two images: the basic image and an image in which the central inner circle was erased. Additionally, each image was presented with the row of circles running horizontally, vertically, or in a tilted position. In experiments 2 and 3, the size of the central inner circle was smaller than in the basic image. Further, to make the configuration of the three circles appear as a first approximation to the shape of a face (Maurer et al. 2002), the position of the smaller central circle was changed in some

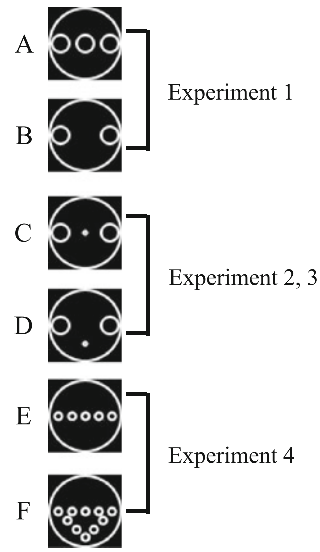

Fig. 1 The *six* images used in the experiment. *A*, a basic image, and *B*, the image in which the central *inner circle* of the basic image was erased, were used in experiment 1. *C*, an image in which the size of the *circle* located in the central *inner circle* was changed to make it smaller than in the basic image, and *D*, one in which the configuration of the *three circles* was changed to a first approximation to the face, were used in experiments 2 and 3. *E*, in which the size of *inner circles* was changed to make it smaller than in the basic image, and *F*, in which *smaller circles* were used with the same configuration as in *D*, were used in experiment 4. All stimuli presented in this figure were oriented horizontally

images to a position close to the outline. We assumed that when the central circle was positioned at the bottom of the display, the configuration was close to an upright face, and when it was positioned at the top, the configuration was close to an inverted face. In experiment 4, the inner circles were smaller than those of the basic image, with the configuration similar to that in experiment 3.

Apparatus

The experiment was conducted inside a darkened soundproof booth. The monkeys were head restrained and seated in a primate chair during the experiment. A scleral search coil was implanted into the eyes to record eye movements. Stimuli were presented on a 22-inch CRT monitor at a distance of approximately 57 cm from the subject. The real-time experimental control system TEMPO (Reflective Computing), running on a dedicated personal computer, was used to generate the stimuli, control the experimental procedure, and record the eye movements.

Procedure

We will first explain the general procedure common to all experiments. The monkeys' task was to make a visual search for a target: the odd element in an array of distracters. Generally, we used two types of orientation for stimulus presentation: the search for a tilted target among horizontal distracters and for a horizontal target among tilted distracters. Further, only in experiment 1, we used a vertical orientation of the inner components. Therefore, the monkeys were required to detect the difference between the orientation of the target and the distracters rather than detecting the difference between other characteristics (e.g., their shape).

The trial began with the presentation of a white circle as the start key at the center of the display. After the monkey fixated its eye on the circle for an average of 2,000 ms (range: 1,500–2,500 ms), both a target and distracters were presented simultaneously on the display and measurements of reaction times were begun. The positions of each stimulus on the screen were selected randomly from 20 possible positions (Fig. 2). The target position was counterbalanced across trials. If the monkey fixated its eye on the target for more than 1,000 ms, a reinforcement (0.2 ml of apple juice) was delivered. Reaction times were defined as the time interval between the onset of the search array and the start point of the correct fixation to the target stimuli. After the delivery of the reward, the inter-trial interval (ITI) began. However, if the monkey fixated its eye on the distracter stimulus for more than 1,000 ms, then the display blackened and the ITI lasted for 10 s. If the subject did not fixate its eye on any object in the display for 20 s, then the ITI was introduced and same trial was repeated. All correct trials were rewarded.

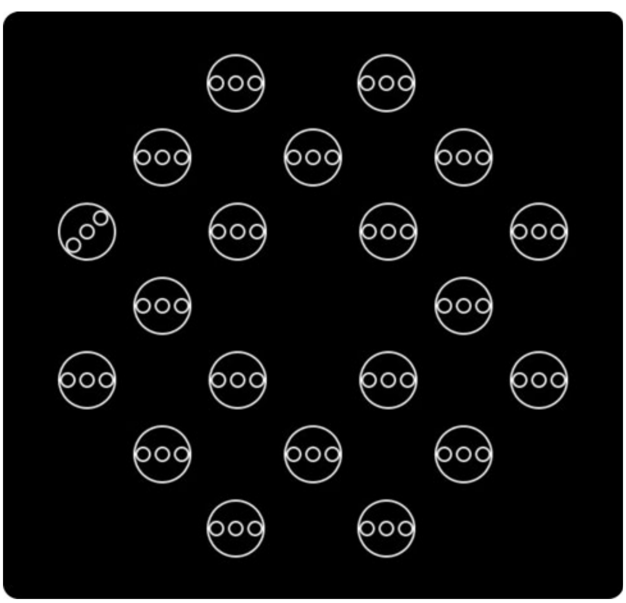

Fig. 2 An example of the actual presentations. The target (positioned at the *upper left*) was a lined object with a tilted orientation and *nineteen* distracters were presented with the same *horizontal* orientation

The experiments consisted of four consecutive blocks, each of which was divided into two experimental phases: a training and a generalization phase. In the training phase, monkeys were trained to search for a target among three distracters in the two different conditions described above (detection of a tilted target among horizontal distracters and vice versa). Both conditions were included within the same session. Each session consisted of 360 trials. These phases were continued until the monkey achieved a criterion of 99 % correct trials in two consecutive sessions. The monkeys were trained for one or two sessions per day.

In the generalization phase, in addition to the task used in the training phase (three distracters), seven, eleven, and nineteen distracters were introduced to test the effect of increasing the number of distracters. Moreover, two new test conditions were introduced. That is, a total of three types of stimulus set were used in each test session. Each set was divided into two conditions depending on the orientation of the target: half of the trials involved the detection of a tilted target (among horizontal/vertical distracters) and the other half involved the detection of a horizontal/vertical target (among tilted distracters). A generalization session consisted of 1,080 trials (720 trials that were the same as the training tasks and 360 test trials: 3 different stimulus sets $\times$ 2 target orientations $\times$ 3 different numbers of distracters $\times$ 20 different positions). The generalization phase was continued for 10 sessions, regardless of the results.

We now describe the procedure of each experiment in detail. In experiment 1, three stimulus sets were used: the combination of tilted and vertical basic stimulus, the combination of tilted and horizontal basic stimulus, and the tilted or horizontal versions of the stimulus with erased central inner circle. The first stimulus set was used in both training and generalization phases, while the other stimulus sets were used only in the generalization phase. Each set was divided into two conditions according to the orientation of the target (tilted or vertical/horizontal) (Fig. 3a).

In experiment 2, the stimulus with a smaller central inner circle was used instead of the basic stimulus. Three stimulus sets were used: the combination of tilted-lined and vertical-lined stimulus, the combination of lined and upright-face stimulus (in both orientations), and the combination of lined and inverted-face stimulus (in both orientations). The first stimulus set was used in both training and generalization phases, and the other stimulus sets were used only in the generalization phase. Each set was divided into two conditions according to the orientation of the target (tilted or horizontal), but in the second and third sets, face-like stimuli were always presented as distracters (Fig. 3b).

In experiment 3, three stimulus sets were used: the combination of tilted-lined and vertical-lined stimulus, the

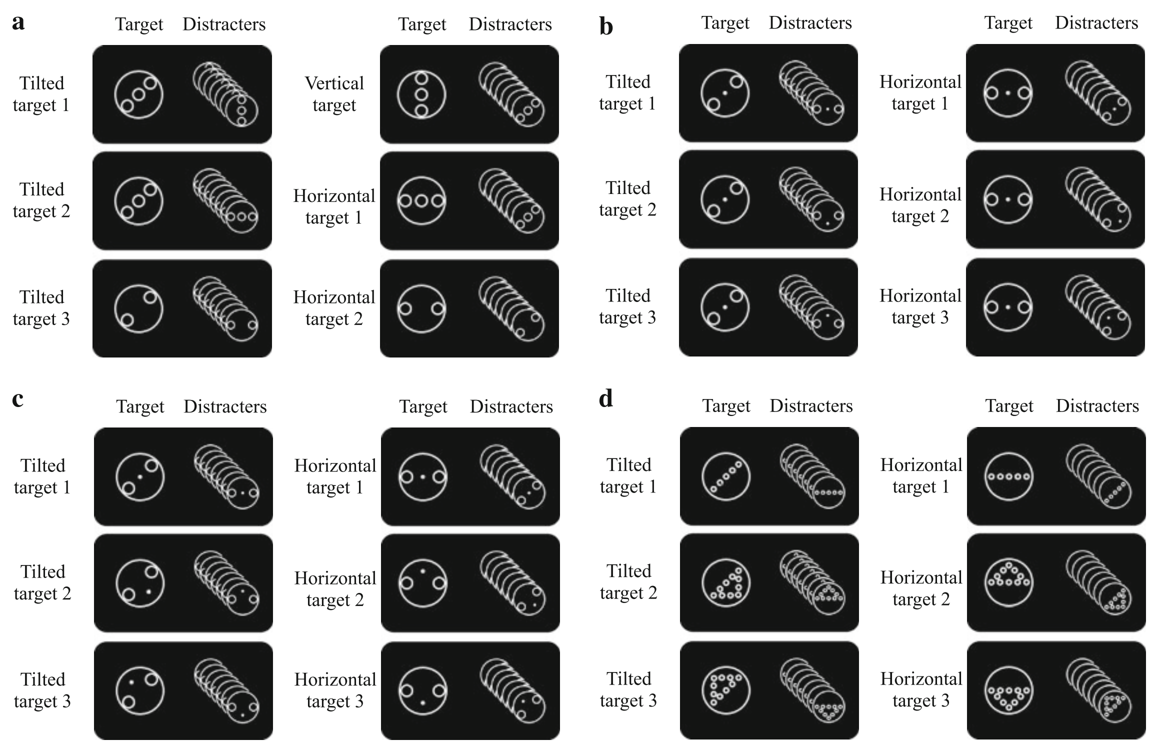

Fig. 3 Examples of the presentation of the target and distracter stimuli in each experiment. *Three tilted* and *three vertical* or *horizontal targets* were presented separately with combinations of particular distracters in experiment 1 (**a**), experiment 2 (**b**), experiment 3 (**c**), and experiment 4 (**d**)

combination of tilted upright-face and horizontal inverted-face stimulus, and the combination of tilted inverted-face and horizontal upright-face stimulus. The first stimulus set was used in both training and generalization phases, and the other sets were used only in the generalization phase. Each set was divided into two conditions according to the orientation of the target (tilted or horizontal) (Fig. 3c).

In experiment 4, although all combinations of stimulus sets and the global configurations of the stimuli were the same as those for experiment 3, the inner circles used in all stimuli were smaller than those of the basic image (Fig. 3d).

Results

Experiment 1

In the training phase, monkeys were trained to search for the target object among three distracter objects. The two monkeys required 32 and 18 sessions, respectively, to satisfy the 99 % criterion. Subsequently, in the generalization phase, the same conditions were introduced along with two additional sets of contrastive conditions, with three different numbers of distracters. The mean correct-response score in the generalization phase (total 10 sessions) was 99.22 % (SE = 1.09).

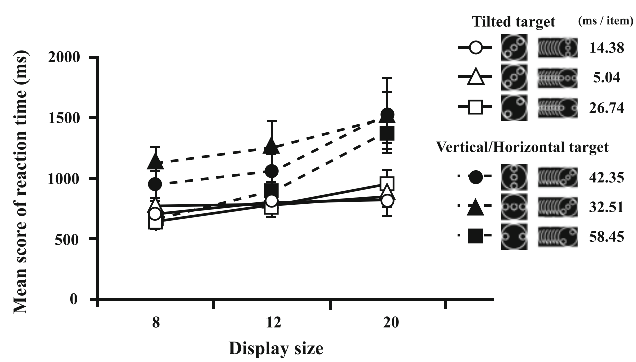

Fig. 4 The mean reaction times measured in experiment 1. Scores are shown for the three display sizes (*8*, *12,* and *20*) with *tilted targets* (*continuous lines*) and with *vertical* or *horizontal target* (*dashed lines*) in three different stimulus conditions (a *circle*, a *triangle*, and a *rectangle*). The *numbers* to the *right* are the slopes of the mean reaction time as a function of array size. *Bars* correspond to standard errors

Figure 4 shows the mean reaction times in the generalization phase. These data were analyzed using a four-way repeated-measures analysis of variance (ANOVA), with the factors of the number of stimuli (the target plus distracters: 8, 12, 20), orientation of the target object (tilted, vertical/horizontal), combinations of stimuli (vertical and tilted, horizontal and tilted, horizontal and tilted with erased central circle), and subject (each five block in two monkeys). The main effects of the number of stimuli ($F_{2,18} = 11.76$, $P < 0.0001$) and the orientation of the target object ($F_{1,9} = 32.58$, $P < 0.0001$) were significant, and a significant interaction was observed between these two main effects ($F_{2,18} = 3.57$, $P < 0.05$). A post hoc analysis (Tukey's HSD test) revealed a significant difference between the numbers of stimuli only in the conditions that had a vertical/horizontal target (and tilted distracters). All other main effects and interactions were insignificant.

An analysis of the slopes of the mean reaction time as a function of array size found a gradient of 14.38 ms per item for trials on which the subjects searched for a tilted target among vertical distracters and 42.35 ms per item for the opposite condition. Further, a gradient of 5.04 ms per item was found for trials on which the subjects searched for a tilted target among horizontal distracters and that of 32.51 ms per item was found for the opposite condition. A gradient of 26.74 ms per item was found for trials on which the subjects searched for a tilted incomplete target among horizontal incomplete distracters and that of 58.45 ms per item was found for the opposite condition.

Experiment 2

The two monkeys required 7 and 4 sessions, respectively, to satisfy the 99 % criterion in the training phase. In the generalization phase, face-like objects were introduced by moving the position of the central inner circle close to the outline. The mean correct-response score in the generalization phase was 99.44 % (SE = 0.53).

Figure 5 shows the mean reaction times in the generalization phase. These data were analyzed using a four-way repeated-measures ANOVA with the following factors: the number of stimuli (the target plus distracters: 8, 12, 20), orientation of the target object (tilted, horizontal), combinations of stimuli (horizontal and tilted lines, horizontal or tilted target and distracters with upright face-like configurations, horizontal or tilted target and distracters with inverted face-like configurations), and subject (each five block in two monkeys). The main effects of the number of stimuli ($F_{2,18} = 25.31$, $P < 0.0001$) and orientation of the target object ($F_{1,9} = 32.58$, $P < 0.0001$) were significant, and a significant interaction was seen between these two main effects ($F_{2,18} = 4.24$, $P < 0.05$). A post hoc analysis revealed a significant difference between the conditions with 20 stimuli and other conditions (8, 12 stimuli) if the target was tilted and a significant difference between the conditions with 20 and 8 stimuli if the target was horizontal. A significant interaction was also observed between the orientation of the target object and combinations of stimuli ($F_{2,18} = 3.90$, $P < 0.05$). A post hoc analysis revealed a significant difference between the two conditions using lined distracters and between those using inverted-face distracters. However, no significant difference appeared between the two conditions using upright-face distracters. Another post hoc analysis among the number of stimuli, orientation of the target object, and combinations of stimuli revealed a significant difference between the conditions with 20 and 8 stimuli if (1) the lined target was tilted and horizontal upright faces were distracters, (2) the lined target was horizontal and tilted lines were distracters, and (3) the lined target was horizontal and tilted inverted faces were distracters. Significant differences were also found between the condition with 20 stimuli and those with 12 and 8 stimuli if the lined target was horizontal and tilted upright faces were distracters.

An analysis of the slopes of the mean reaction time as a function of array size found a gradient of 5.38 ms per item for trials on which the subjects searched for a tilted-lined target among horizontal-lined distracters and 26.77 ms per item for the opposite condition. Furthermore, a gradient of 39.75 ms per item was found for trials on which the subjects searched for a tilted-lined target among horizontal upright-face distracters and that of 47.84 ms per item was found for trials on which the subjects searched for a horizontal-lined target among tilted upright-face distracters. A gradient of 13.93 ms per item was seen for trials on which the subjects searched for a tilted-lined target among horizontal inverted-face distracters and that of 58.45 ms per item was observed for trials on which the subjects searched for a horizontal-lined target among tilted inverted-face distracters.

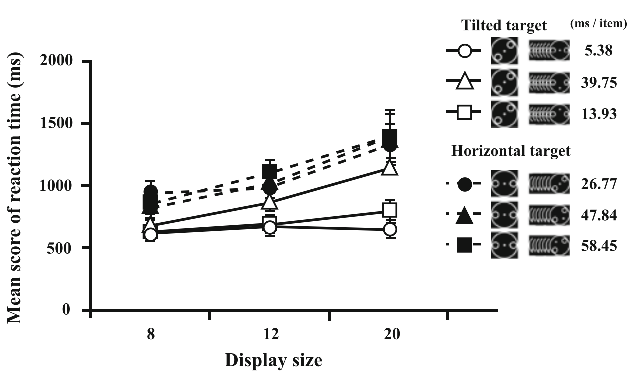

Fig. 5 The mean reaction times noted in experiment 2. Scores are shown for the three display sizes with two different targets and three stimulus conditions, as in experiment 1. The *numbers* to the *right* are the slopes of the mean reaction time as a function of array size. *Bars* correspond to standard errors

Experiment 3

After the monkeys were trained using the same stimuli as in experiment 2, face-like objects were introduced for both the target and distracter stimuli. The mean correct-responses score in the generalization phase was 99.11 % (SE = 1.08).

Figure 6 shows the mean reaction times in the generalization phase. These data were analyzed using a four-way repeated-measures ANOVA with the following factors: the number of stimuli (8, 12, 20), orientation of the target object (tilted, horizontal), combinations of stimuli (tilted-lined non-face target among horizontal-lined non-face distracters and vice versa, tilted upright-face target among inverted horizontal-face distracters and vice versa, tilted inverted-face target among horizontal upright-face distracters and vice versa), and subject (each five block in two monkeys). The main effects of the number of stimuli ($F_{2,18} = 34.36$, $P < 0.0001$), orientation of the target object ($F_{1,9} = 22.02$, $P < 0.0001$), and combination of stimuli ($F_{2,18} = 10.17$, $P < 0.0001$) were significant. A significant interaction existed between the orientation of the target object and combination of stimuli ($F_{2,18} = 1.63$, $P < 0.05$). A post hoc analysis revealed a significant difference between conditions with tilted targets and with horizontal targets in each combination of stimuli. Notably, however, no significant differences were found among the following conditions: a tilted non-face target among horizontal non-face distracters, a tilted upright-face target among horizontal inverted-face distracters, and a horizontal upright-face target among tilted inverted-face distracters. Furthermore, no significant differences were observed among the following conditions: a horizontal non-face target among tilted non-face distracters, a horizontal inverted-face target among tilted upright-face distracters, and a tilted inverted-face target among horizontal upright-face distracters. Another post hoc analysis among the number of stimuli, orientation of the target object, and combinations of stimuli revealed a significant difference between the condition with 20 stimuli and those of 8 and 12 stimuli if a tilted inverted face was the target and horizontal upright faces were distracters. Further, significant differences were found between the condition with 20 stimuli and that with 8 stimuli if (1) the target was a horizontal line and the distracters were tilted lines and (2) if the target was horizontal inverted face and the distracters were tilted upright faces.

An analysis of the slopes of the mean reaction time as a function of array size found a gradient of 11.97 ms per item for trials on which the subjects searched for a tilted-lined (non-face) target among horizontal-lined (non-face) distracters and 39.86 ms per item for the opposite condition. Further, a gradient of 14.95 ms per item was found for trials on which the subjects searched for a tilted upright-face target among horizontal inverted-face distracters and that of 34.60 ms per item was found for the opposite condition. Furthermore, a gradient of 33.60 ms per item was found for trials on which the subjects searched for a tilted inverted-face target among horizontal upright-face distracters and that of 10.14 ms per item was found for the opposite condition.

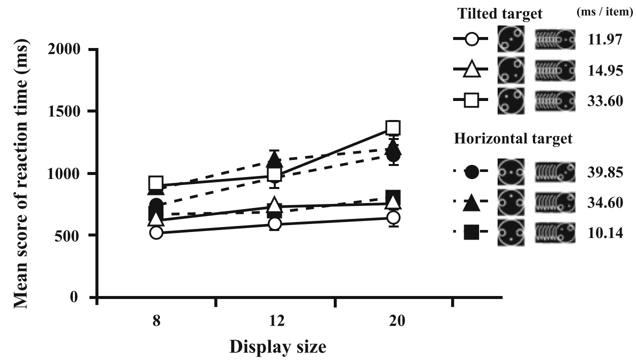

Fig. 6 The mean reaction times observed in experiment 3. Data are presented as in experiments 1 and 2. The *numbers* to the *right* are the slopes of the mean reaction time as a function of array size. *Bars* correspond to standard errors

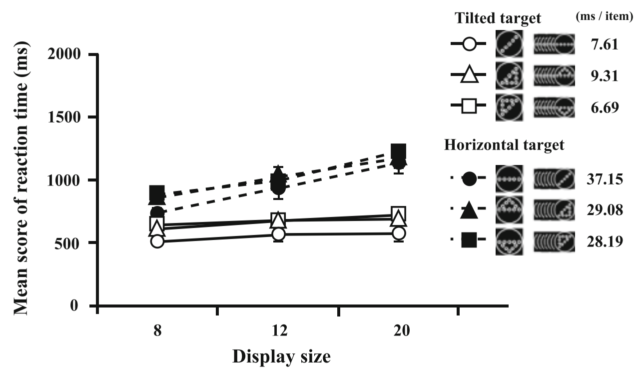

Fig. 7 The mean reaction times recorded in experiment 4. Data are presented as in experiments 1 and 2. The *numbers* to the *right* are the slopes of the mean reaction time as a function of array size. *Bars* correspond to standard errors

Experiment 4

In experiment 4, although the global configurations of the stimuli in all conditions were the same as in experiment 3, more inner circles with a smaller size were used. The two monkeys required 12 and 8 sessions, respectively, to satisfy the 99 % criterion in the training phase. Subsequently, the mean correct-responses score in the generalization phase was 99.11 % (SE = 0.93).

Figure 7 shows the mean reaction times in the generalization phase. These data were analyzed using a four-way repeated-measures ANOVA with the following factors: the number of stimuli (the target plus distracters: 8, 12, 20), orientation of the target object (tilted, horizontal), combinations of stimuli (horizontal and tilted lines, horizontal upright and tilted inverted triangles, horizontal inverted and tilted upright triangles), and subject (each five block in two monkeys). The main effects of the number of stimuli ($F_{2,18} = 27.83$, $P < 0.0001$) and orientation of the target object ($F_{1,9} = 249.99$, $P < 0.01$) were significant, and a significant interaction was found between these two main effects ($F_{2,18} = 12.03$, $P < 0.05$). A post hoc analysis revealed a significant difference between the numbers of stimuli only in the conditions that had a horizontal target among tilted distracters. All other main effects and interactions were insignificant.

An analysis of the slopes of the mean reaction time as a function of array size found a gradient of 7.61 ms per item for trials on which the subjects searched for a tilted-lined target among horizontal-lined distracters and 37.15 ms per item for the opposite condition. A gradient of 9.31 ms per item was found for trials on which the subjects searched for a tilted downward triangle target among horizontal upward triangle distracters and that of 29.08 ms per item was found for the opposite condition. Furthermore, a gradient of 6.69 ms per item was observed for trials on which the subjects searched for a tilted upward triangle target among horizontal downward triangle distracters and that of 28.19 ms per item was seen for the opposite condition.

Discussion

Overall, the monkeys scored almost 100 % correct in the generalization phases. Therefore, we will discuss their reaction times rather than their correct response rates. In experiment 1, searching for a tilted target among vertically or horizontally positioned distracters showed slightly increased reaction times when the number of distracter stimuli was increased. In contrast, searching for a vertically or horizontally positioned target among tilted distracters showed a large and significant increase in reaction times whenever the number of distracter stimuli was increased. This result suggests that Japanese monkeys showed the difference between the two search tasks related to a measure of the efficiency of the search. In other words, at least in the situation where the monkeys were detecting the difference between the orientations of the objects, they clearly showed a search asymmetry similar to both humans and chimpanzees. Previous studies in humans have used the slope of the increase in reaction time to detect the target among additional distracter items as a measure of search efficiency, with a slope close to zero in efficient parallel search and a slope of about 25–35 ms or more per item in inefficient serial search (Wolfe 2001). Our results also showed this trend relatively well, except in the condition in which the central inner circle was erased. These results suggest the possibility that monkeys can search for a tilted line among horizontal/vertical lines in a parallel manner; in the opposite conditions, they search in a serial manner.

In experiment 2, the detection of a target among distracters was examined, similar to that in experiment 1, but new stimulus sets replaced those used in the previous experiment. When the central circle of the distracter stimulus was made smaller, the search remained efficient. However, when the central circle of the distracter stimulus was changed to form the configuration of an upright face (positioned downward), the search efficiency decreased, even when the target stimulus was tilted. That is, the search asymmetry observed in experiment 1 was affected by the existence of the upright face. On the other hand, when the inverted-face configuration (positioned upward) was used, the search remained efficient. Additionally, no difference appeared in search efficiency for the detection of a horizontal line among both tilted upright and tilted inverted faces. These results indicate two points. First, relatively more complex visual information, such as an upright face, was significantly related to the monkeys' search efficiency. Second, the power of the upright-face distracter to interrupt the search for the target was variable and dependent on the target orientation. Although the upright-face distracters as compared with the inverted-face distracters effectively interrupted the monkeys' search for the target when searching for a tilted line (which was searched efficiently in experiment 1), if a horizontal object (which was searched inefficiently in experiment 1) was the target, there was nothing remarkable about the upright-face distracter and both types of faces worked equally well as distracters. These results suggest that the upright-face information, previously described as upright-face specialization (Tomonaga 2007) or the inversion effect (Yin 1969), was clearly meaningful in the earlier stage of visual search rather than in the later stages. In other words, although an upright face was a distinctive feature as compared with an inverted face, the distinctiveness may be more powerful in the situation of efficient search. Therefore, upright-face distracters may interrupt the efficient search for a tilted-line target (a basic feature).

More interestingly, prior to the experiments, our monkeys had never experienced the face-like stimuli that were used in these experiments. This means that the ability of upright-face distracters to disturb the search efficiency may arise from their innate abilities or from abilities acquired in their daily lives rather than from the learning of particular experimental conditions, or it could come from a very early developmental stage (Kuwahata et al. 2004; Sugita 2008).

In experiment 3, not only the distracter stimulus but also the target stimulus was changed to contain the face-like configurations in some conditions. The search for a tilted line among horizontal lines remained efficient. Furthermore, the search for both tilted and horizontally oriented upright-face targets among inverted-face distracters was relatively efficient, but that for an inverted-face target among upright-face distracters was inefficient, regardless of their orientation (tilted or horizontal). Although it remains uncertain whether monkeys can detect the basic feature—tilted lines—in our face stimulus, as we suggested in the closing lines of the discussion of experiment 2, each tilted or horizontal upright-face distracter interrupts the efficient target search again. Moreover, when each tilted and horizontal upright face was the target, each upright face was searched as efficiently as was a tilted-line target among horizontal line distracters. It may safely be assumed that the upright face, like other basic features, was a very powerful stimulus for efficient search by monkeys.

We must consider more carefully that the face stimulus commonly contained information for both relatively high-level representations, which were clearly divided between the face and other objects, and relatively low-level visual features, which could be shared between the face and other objects (Nothdurft 1993; VanRullen 2006). Certainly, our face stimuli also contained information for both. While we consider them as faces according to their configurations, we can also consider them as a group of circles or as the form of a triangle. However, in experiment 4, monkeys did not show the search asymmetry toward objects that had the form of a triangle. From this result, it can be concluded that simple visual features related to the form of a triangle, or the top-heavy bias (Simon et al. 2001) that has often been discussed in relation to human infants, cannot account for the results. It seems reasonable to suppose that configural information unique to the face may account for the monkeys' search asymmetry for faces. Further consideration is needed to identify the features that are critical for animals' search asymmetry for faces.

It should be emphasized that the results found in macaques, a type of old world monkey, showed not only a difference between upright and inverted faces (upright superiority of the face relative to the inverted face) but also sufficient evidence of visual search asymmetry to discuss whether visual search is processed in a parallel or a serial manner. As we have seen, monkeys showed two different trends of search efficiency for the detection of a tilted or vertical/horizontal-lined object. The results of experiments 2 and 3 also showed two distinctive trends, similar to that observed in experiment 1, one being a slope of less than 20 ms, a relatively flat slope, and the other, a slope of more than 25 ms. The upright-face targets in experiment 3 showed low slopes, while the conditions including horizontal no-face targets and those including upright-face distracters showed high slopes.

The differences in the trends reported in most previous studies of facial search in humans, in particular when schematic faces were used, have not been discussed in terms of the difference between serial and parallel search strategies but rather as those in degree within serial search strategies. This is because both easy and hard searches often showed the slope of more than 25 ms described above. However, certain experiments in humans used a real face target among many types of real objects and showed a more efficient search slope, which was sufficient to suggest a parallel strategy (Hershler and Hochstein 2005).

There is room for further investigation of whether both parallel and serial strategies are used for facial search, but the main conclusion of the present study is the possibility that Japanese monkeys can detect a tilted-line target and a schematic upright-oriented face using two different strategies. Furthermore, the flat slopes observed provide sufficient evidence to suggest the existence of a rapid, parallel, pre-attentive strategy in the visual search task.

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