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Contrasting the Edge- and Surface-Based Theories of Object Recognition: Behavioral Evidence From Macaques (*Macaca mulatta*)

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Abstract

This study assessed the contribution of edge and surface cues on object representation in macaques (*Macaca mulatta*). In Experiments 1 and 2, 5 macaques were trained to discriminate 4 simple volumetric objects (geons) and were subsequently tested for their ability to recognize line drawings, silhouettes, and light changes of these geons. Performance was above chance in all test conditions and was similarly high for the line drawings and silhouettes of geons, suggesting the use of the outline shape to recognize the original objects. In addition, transfer for the geons seen under new lighting was greater than for the other stimuli, stressing the importance of the shading information. Experiment 3, using geons filled with new textures, showed that a radical change in the surface cues does not prevent object recognition. It is concluded that these findings support a surface-based theory of object recognition in macaques, although it does not exclude the contribution of edge cues, especially when surface details are not available.

Keywords

object recognition; macaque; behavior; geon; surface-based theory

The ability of nonhuman primates to perceive and recognize pictorial objects has been widely investigated in behavioral studies using several procedures, such as spontaneous responses to pictures (e.g., Sackett, 1965), categorization tasks (e.g., Schrier & Brady, 1987), and discrimination tasks (e.g., Jitsumori, 1994). Thus far, these nonhuman primate studies have focused their attention on the cognitive abilities involved during picture perception but have neglected the issue of which feature(s) is required to recognize the objects of the pictures. More is known of this issue in humans from numerous studies aimed at understanding how an observer perceives three-dimensional (3D) shapes of objects from

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two-dimensional (2D) patterns of light that project onto the retina. That human literature has led to two main object-recognition theories: a “structural description” theory and a “viewer-based” theory.

According to the structural description theory, the edges of an object are sufficient for its recognition (Biederman, 1987). Biederman and Ju (1988) suggest that, for humans, line drawings alone yield enough information for normal object recognition; therefore, that the internal features of the object, such as its color, texture, and shading, are of minimal importance. Some studies have demonstrated that the shape of an object could be retrieved from its silhouette without any information about surface details (e.g., Hayward, Tarr, & Corderoy, 1999). However, this claim seems to be accurate only as long as the silhouette clearly depicts the object's parts. Hayward, Wong, and Spehar (2005) found that silhouettes do not always allow for view generalization as efficiently as do shaded images, especially when objects are less complex (for instance, objects that contain few components).

Alternatively, the viewer-based theory proposes that the details of an object are stored in memory, even if they are not necessary for its recognition (Tarr & Pinker, 1990). Tarr, Kersten, and Bülthoff (1998) explored the effects of changing the direction of the lighting in an object-recognition task. People were significantly faster to process an object with the light source remaining in the same location compared with an object seen under a moving source of light. They concluded that surface information, such as shading information, was stored in the object representation. In addition, some studies have highlighted the role of surface details, such as the texture, in object recognition (e.g., Price & Humphreys, 1989).

An important point is that edge- and surface-based theories of object recognition allow different predictions concerning the effects of surface information on recognition. Edge-based accounts predict that surface information may not have any effect on object recognition (at least when the edge details are salient). Thus, the recognition of line drawings, containing no surface details, should be as efficient as that of complete pictures of objects. In contrast, surface-coding accounts predict that recognition will benefit if objects are depicted along with their surface details, such as variations in brightness, texture, and color.

In the next section, we present evidence from behavioral and neurophysiological studies in nonhuman primates that could disentangle these two theories. Unfortunately, data from behavioral investigations on picture recognition in nonhuman primates are conflicting. Object recognition likely depends on several experimental factors, such as the experience of the subject with the picture (e.g., language-trained animals, picture-naïve animals, picture-experienced animals), the physical characteristics of the pictures (e.g., its size, the quality of the depiction), and even the procedure used to test the animal (spontaneous responses or acquired responses). Davenport, Rogers, and Russel (1975) trained five chimpanzees in a haptic-to-visual cross-modal experiment with real objects. They found that four chimpanzees were able to match-to-sample when the sample was a black-and-white photograph or a line drawing. However, cross-modal perception was better with photographs than with line drawings. The most convincing case of successful transfer in apes, from fully detailed pictures to line drawings, is the experiment of Itakura (1994). This study

demonstrated the ability of a chimpanzee named Ai, with extensive training for visual symbols use, to recognize and to label familiar individuals portrayed in line drawings. Zimmermann and Hochberg (1970) trained infant rhesus monkeys to discriminate real objects before testing them with photographs and outline figures of these objects. Monkeys made consistent responses to pictorial representations of the stimuli (photographs or drawings). Although internal shadow cues enhanced transfer performance, that feature was not mandatory. These experiments suggest that nonhuman primates can recognize pictorial objects that lack surface cues.

These findings, however, contrast with other behavioral studies that failed to demonstrate that nonhuman primates are able to transfer from a real object to its 2D black-and-white photograph or line drawing depiction. Winner and Ettlinger (1978) trained two pictorially naïve chimpanzees in a matching-to-sample task. The subjects first had to match real objects with real objects and subsequently objects with their photographs (color full size or black-and-white photographs). Initially, chimpanzees were unable to perform the objects–photographs task successfully, with performance remaining at chance level for the first 4 days of testing and then rising moderately, but not consistently, above chance. These results suggest that for inexperienced apes, the loss of features, such as 3D cues, impaired recognition of the pictorial object. In the study by Tolan, Rogers, and Malone (1981), two adolescent rhesus monkeys were trained on visual-to-haptic matching to sample or haptic-to-visual matching to sample with black-and-white photographs, silhouettes, and outline drawings of the real objects. Monkeys performed well with the black-and-white or silhouette photographs but not with the outline drawings, suggesting that features such as texture and shadows were important to recognize a represented object. Taken together, these behavioral studies provide no clear conclusion on the critical features for object recognition.

Inspection of the literature reveals that neurophysiological studies in nonhuman primates have been more focused than behavioral studies on the characteristics of the pictorial object allowing its recognition. In monkeys, object recognition was mostly studied by exploring the visual selectivity of specific brain areas, especially the inferior temporal cortex (IT), as this structure plays an important role in visual discrimination learning and retention (Dean, 1976). Several studies suggest that IT is selective for the shape, color, texture, and luminance contrast of 2D objects. In anesthetized macaques, Desimone, Albright, Gross, and Bruce (1984) recorded IT neurons' responding to simple stimuli (e.g., edges and bars) or to highly complex stimuli (e.g., flowers and faces). Once a neuron responded to a particular stimulus, they tried to isolate the critical features underlying that response. They observed that most of the selective neurons were sensitive to the stimulus shape, color, or texture, or a combination of the three. Other studies have suggested that IT is involved in the processing of shape *and* surface information, such as the color, texture, shading, and contrast of 3D represented objects (e.g., Kovacs et al., 2003). Altogether, IT neurons appear sufficiently sensitive to represent the 3D structure of many real-world objects. However, electrophysiological experiments suffer from two main limitations. The first of these is the poverty of the task demands in these studies. Indeed, when monkeys are not anesthetized, they are at best engaged in a fixation task. This low-demanding task limits the potential influence of top-down processes. The second limitation is the difficulty of correlating the

neuronal and the behavioral responses. According to recent neuroimaging studies, the representation of an object is not necessarily restricted to a region that responds maximally to that object, but rather is distributed across a broader expanse of cortex (e.g., Sereno, Trinath, Augath, & Logothetis, 2002). Despite the valuable information provided by the recording of neuronal activity, it is unclear whether the findings from these studies would reflect neural mechanisms in more demanding tasks as those used in behavioral studies. That limitation prevents firm conclusions on the validity of any object-recognition theory.

In that theoretical context, our study assessed in three complementary experiments whether monkeys rely on contours or internal surface cues while learning grayscale volumetric objects (referred to as *geons*; Biederman, 1987). The purpose of the first experiment was to test the two theories of object recognition by assessing the pictorial characteristics on which macaques rely during object recognition. Our hypothesis was that if object recognition is accounted for by an edge-based representation, then macaques should be able to recognize objects depicting inner contours or outline shape (i.e., line drawings or silhouettes). Conversely, if object recognition is more in agreement with a surface-based theory, macaques should be better in the recognition of an object containing some surface cues (i.e., light change stimulus). Five macaques were trained to discriminate four polyhedral geons (edged geons) in a four-alternative forced-choice task. Transfer of performance was then assessed after training with the line drawings of the original geons, their silhouettes, and the original geons seen under a change in the direction of illumination (light change stimulus). The aim of the second experiment was to determine whether the characteristics on which macaques rely to memorize a represented object were dependent on the shape of the geon. In contrast to Experiment 1, using polyhedral objects (called edged geons), for which the position of the inner contours was insensitive to illumination changes, Experiment 2 used smoothed objects, more representative of the natural objects, for which the position of these inner contours is continually displaced according to the light orientation. Our hypothesis was that if object recognition depends on edge-based representations, then macaques should be impaired in the recognition of a smoothed geon seen under a light change. The last experiment was aimed at determining whether the macaques could reconstruct an original object from a new pattern of texture, radically different from the memorized surface cues. Our rationale was that if monkeys rely on edge-based representations, then the alteration of the surface cues should have minimal effect on their recognition performance. To test this hypothesis, we trained macaques to discriminate four new geons and were tested with two different textural changes.

General Method

Subjects

The same five male rhesus monkeys (*Macaca mulatta*) were tested in the three experiments; Willie (22 years old), Gale (24 years old), Chewie and Luke (both 8 years old), and Han (5 years old). They were not food deprived or weight reduced, and they were given their usual daily diet and continuous access to water. The monkeys were already highly familiar with the joystick apparatus at the beginning of the experiment and with the alternative forced-choice task procedure used in that experiment (see Washburn, 1993).

Apparatus

All monkeys were tested in their home cages with 24-hr access to the test apparatus, working or resting as they preferred. All the experiments used the Language Research Center's Computerized Test System (see Richardson, Washburn, Hopkins, Savage-Rumbaugh, & Rumbaugh, 1990, for a complete description of the system). This system allows each monkey to manipulate the joystick outside of its cage through the cage mesh, with its head positioned approximately 30 cm from the computer screen. The joystick controlled the displacements of a cursor on this color computer monitor (17 in.). The food dispenser (interfaced to the computer using a relay box and output board) delivered 94-mg fruit-flavored food pellets in accordance with the prevailing reinforcement contingencies.

Stimuli

All the stimuli were created with Catia V5R15 Dassault System, using the 200-dpi setting and described in the *Stimuli* section of each experiment.

General Procedure

The general procedure was inspired by Young, Peissig, Wasserman, and Biederman, (2001). Depending on the Language Research Center experimental planning, monkeys were tested either for 4 or 8 continuous hr 3 times a week, or for 24 continuous hr once a week. All the experiments consisted of two phases: training and testing. Each trial began with the presentation of one geon (S +) located in the center of the screen and the cursor (a red circle 0.5 cm in diameter) centered at the bottom of the screen. The monkey had to move the joystick to put the cursor in contact with the geon (S +). Then, four colored circles corresponding to the sample stimuli (4.5 cm in diameter; green, blue, purple, red) appeared in each corner of the screen with their starting locations counterbalanced across trials. The monkey was requested to bring the cursor in contact with one of the sample stimulus in response to the actual display (S +). There was no time limit for responding. Positive reinforcements consisted of the delivery of a food reward paired with a melodic tone. By contrast, incorrect responses were followed by a 10-s timeout during which the screen turned completely blank and a buzz tone sounded. The next trial was presented immediately after the delivery of the reinforcement or timeout.

During the training phase, the monkeys were trained to associate one of the four corner colored response stimuli with each of the four single geon objects. The assignment of a geon to a particular response stimulus was constant throughout the experiment. During that phase, the monkeys were presented with a session of 100 trials, with 25 trials for each geon appearing randomly and differentially reinforced according to the response. Each monkey was required to meet a session criterion of 80% correct for each of the four geons and of 85% correct overall before it could proceed to testing. Because there was no time limit for responding, the monkey's response was mandatory and what we considered as an error was necessarily a wrong response.

During the test phase, one session consisted of baseline trials (with the presentation of the four geon training stimuli) differentially reinforced according to the response and nonreinforced test trials. All the test phases lasted until each monkey had received 15

sessions. Notably, if a monkey failed to reach the criterion of 85% overall and 80% for each training geon from the baseline trials, it was returned for training sessions until it met again that criterion.

Experiment 1

In the first experiment, our objective was to compare how well macaques generalized their discriminative responding from training stimuli to the test stimuli to assess the validity of the two main theories of object recognition (Biederman, 1987; Tarr & Pinker, 1990). The five macaques were thus trained to discriminate four edged geons in the four-alternative forced-choice task described above, and then were tested for their ability to recognize the same geons after three different modifications. First, the original geons were transformed into line drawings, containing only some information about the objects' orientation and depth discontinuities (inner contours and outline shape). Second, the same original geons were seen as silhouettes, constituted by the filled bounded contour of the objects without inner contours, like in a backlit situation (i.e., against the light). And finally, the transfer of performance was tested with the original geons seen under a change in the direction of illumination (approximately 90°). Changing the direction of an object's illumination alters the luminance variation of this object, whereas the outline shape of the object and its internal image edges remain unchanged.

According to the edge-based theory of object recognition, macaques should have the same level of performance with the line drawings, the silhouettes, and the objects seen after a change in the light direction. Indeed, this theory predicts that edge information (inner contours *or* outline shape) is used to recognize an object, and all our test stimuli contained one or the other information. In contrast, the surface-based theory predicts that presence of surface cues, such as the luminance variation, should help the macaques in object recognition, and thus favors identification of the light change test stimuli over the other test stimuli.

Method

Stimuli—Stimuli were a truss, a brick, a wedge, and a prism, as seen in Figure 1—Experiment 1, A, B, C, D (the truss, in fact, comprised two geons but was called “a geon”). As inferred from the viewing distance (monkey's head was positioned approximately 30 cm from the monitor), the training stimuli ranged in size from 10.1 to 15.4 visual degrees in width (i.e., 5.3 to 8.1 cm) and 14.3 to 16.7 visual degrees in height (i.e., 7.5 to 8.8 cm). The total surface of each geon was, respectively, 32.8 cm², 55.2 cm², 32.6 cm², and 44.9 cm² for geons A, B, C, and D. The average grayscale for each geon was, respectively, equal to 104, 120, 111, and 100 for geons A, B, C, and D, according to the grayscale saturation that could range from 0 for white to 255 for black.

The test stimuli consisted of line drawing, silhouette, and light change condition stimuli as illustrated in Figure 1—Experiment 1, A', A'', A'''. The line drawings were rendered by erasing the internal surface of each stimulus so that only the edges (outline shape and inner contours) remained. The silhouettes were rendered by replacing the internal structure of each stimulus with a 158 grayscale level. The light change stimuli were rendered by changing the

illumination direction approximately 90°. The shadings were different under the new condition of illumination so that the grayscale level for each geon was slightly modified (128, 118, 122, and 108 for A, B, C, and D, respectively).

Procedure—After the training phase, the monkeys were given 15 test sessions, each consisting of 124 trials: 100 differentially reinforced baseline trials (with the presentation of the four geon training stimuli) and 24 nonreinforced test trials. These 24 test trials correspond to the presentation of the three test versions (the line drawing, the silhouette, and the light change modification) of each object (A, B, C, and D), presented twice within a single session.

Results

The monkeys required a mean of 124.6 sessions ($SEM = 23.9$) to reach the training criterion. In the testing phase, they performed well with the training stimuli ($M = 90.6\%$), and although they exhibited an overall decrement in accuracy for all the three types of test stimuli (see Figure 2), all the monkeys responded above chance (25%) in each condition. Table 1 reports the results of individual one-tailed binomial tests calculated on the scores of each individual (defined as the number of correct responses) and in each test condition (line drawing, silhouette, and light change stimuli).

To ascertain that the absence of reinforcement for the test trials did not influence monkeys' performance within and across the test sessions, we conducted two analyses on the pooled responses of the five monkeys. We compared scores of the first and the second test trials for the 12 test stimuli of the 15 averaged sessions (one-way repeated analysis of variance, [ANOVA]) to test a possible within-session effect of learning. Results revealed no difference between first and second test trials, $F(1, 4) = 0.574$, $p = .49$ (see Figure 3A). To evaluate a potential across-sessions effect, we also ran a one-way ANOVA on the average responses for the 12 test stimuli, considering the session ($n = 15$) as the unique factor. Again, the performance did not improve across test sessions, $F(14, 56) = 0.227$, $p = .99$ (see Figure 3B). These analyses confirmed that the absence of reinforcement in test trials did not affect the responses of the monkeys as the performance stayed relatively constant within and across sessions.

We next conducted a one-way repeated ANOVA on the scores, with each stimulus type (training, line drawing, silhouette, and light change stimuli). This analysis revealed a significant main effect of stimulus type, $F(3, 12) = 80.27$, $p < .001$. In addition, a Tukey post hoc analysis indicated that the training stimuli were the best recognized ($p < .001$) and provided the following pattern of results for the test stimuli: Light change stimuli were better recognized than silhouette and line drawing stimuli ($p < .001$), but there was no difference between silhouettes and line drawings ($p > .05$; see Figure 2).

Discussion

One first very interesting result is that macaques, although they exhibited a decrement in recognition compared with training stimuli, performed above chance for the three types of test stimuli. This result means that macaques trained with realistic illuminated geons

exhibited significant transfer to objects showing only inner contours and outline shape, or outline shape alone, or objects with an alteration of the luminance variation.

The next interesting result is that performance varied depending on the stimulus type. The lack of difference between the performance obtained with the line drawings and the silhouettes of geons suggests that the macaques did not rely on the inner contours information provided by the line drawings, but rather focused their attention on the outline shape, information shared by both test stimuli. In addition, the performance with geons submitted to a change in the direction of illumination provides two major pieces of information. The first is that the internal surface information, such as texture and shading, favored the original object recognition compared with the information of the inner contours and the outline shape. The second is that the learned representation of the original object appears to be highly stimulus specific given that the geons submitted to light changes yielded lower performance than the training ones.

Unfortunately, definitive conclusions remain impossible at this point. One limitation of Experiment 1 is that the position of the inner contours remained constant across light changes, and could thus have been used by the macaques to recognize the object submitted to a light change. It, therefore, appears too premature to completely exclude the role of the inner edges in object recognition. To investigate this issue, we designed and used some smoothed geons in Experiment 2, with the physical particularity of having the position of their inner contours vary after a change in the direction of the illumination.

Experiment 2

The same five macaques as before were trained to discriminate four new smoothed geons in the four-alternative forced-choice task. After training, transfer of performance was assessed by using the line drawings and silhouettes of the original geons and the same geons after a change in the direction of illumination. Our hypothesis was that if macaques rely more on edge-based representations, they should be impaired in the recognition of a smoothed geon seen under a light change. Indeed, the position of the apparent inner edges created by the shading in these smoothed geons is sensitive to illumination changes and cannot be exploited by the macaques as visual cues to perform object recognition of the test stimuli. By contrast, if object recognition is more dependent on surface-based representations, the pattern of performance should be the same with edged and smoothed geons seen under a light change.

Method

Stimuli—Stimuli for the second experiment consisted of a pear, a barrel, a noodle, and a cone, as illustrated in Figure 1—Experiment 2, A, B, C, D. As inferred from the viewing distance, the training stimuli ranged in size from 11.6 to 16.9 visual degrees in width (i.e., 6.1 to 8.9 cm) and from 15.6 to 18.4 visual degrees in height (i.e., 8.2 to 9.7 cm). The total surface of each geon was, respectively, 51.1 cm², 47.2 cm², 26.5 cm², and 29.5 cm² for geons A, B, C, and D. The average grayscale for each geon was approximately similar (83, 104, 71, and 78 for A, B, C, and D, respectively) according to the grayscale saturation that could range from 0 for white to 255 for black.

The test stimuli of the second experiment consisted of line drawing, silhouette, and light change stimuli and were rendered following the same process as in Experiment 1 (see Figure 1—Experiment 2, A, A', A'', A'''), that is, the line drawings were rendered by erasing the internal surface of each stimulus, and the silhouettes by replacing the internal structure of each stimulus with a 158 grayscale level. The light change stimuli were rendered by changing the illumination direction approximately 45°. That angle prevents depiction of the geons as silhouettes. This new condition of illumination made each geon darker because of the shape of the geons (grayscale level = 132, 132, 127, and 131 for geons A, B, C, and D, respectively).

Procedure—After having reached the learning criterion at the end of the training phase, the macaques were given 15 test sessions, each consisting of 124 trials: 100 differentially reinforced baseline trials (with the presentation of the four geon training stimuli) and 24 nonreinforced test trials. The 24 test trials of each session used the three versions (line drawing, silhouette, and light change) of each object (A, B, C, and D), each being presented twice within a single session.

Results

For the monkeys, reaching the training criterion was easier than in Experiment 1 ($M = 40.8$ sessions, $SEM = 2.75$). They all performed above chance (25%) in all the test conditions (see Figure 4). Table 2 shows the percentage of correct responses for each monkey, their scores, and the results of one-tailed binomial test calculated for each subject and test condition.

Again, we confirmed that the nonreinforcement procedure employed for the test trials did not account for the pattern of results obtained. We conducted a one-way repeated ANOVA on the scores of the first and second test trials, averaged over the 15 test sessions, the 12 test stimuli, and the five monkeys (within-session condition). We also ran an ANOVA comparing performance across the 15 test sessions, the 12 test stimuli, and the five monkeys (across-sessions condition). Results of both analyses did not reveal either a learning effect between first and second test trials, $F(1, 4) = 0.013, p = .915$ (see Figure 5A), or across-session improvement, $F(14, 56) = 1.269, p = .255$ (see Figure 5B). In addition, when the individuals were considered, two monkeys slightly improved their performance across sessions, $F(14, 154) = 1.85, p < .05$, and $F(14, 154) = 3.69, p < .001$, respectively, for Monkeys 2 and 3, but this effect did not emerge for the remaining three monkeys.

Scores were submitted to a one-way repeated ANOVA, with each stimulus type (training, line drawing, silhouette, and light change stimuli). This revealed a significant main effect of stimulus type, $F(3, 12) = 33.39, p < .001$. A Tukey post hoc analysis indicated that the training stimuli were more easily recognized than the test stimuli ($p < .001$). In addition, results provided the same pattern as in Experiment 1 with the edged geons, that is, the light change stimuli were better recognized than the line drawing stimuli ($p < .001$), but there was no difference between silhouette and line drawing stimuli ($p > .05$; see Figure 4).

Discussion

Use of smoothed geons fits the pattern of performance obtained with the edged geons in Experiment 1, namely, that the three types of test stimuli were recognized above chance and followed the previous reported profile of performance. A qualitative comparison between performance obtained with the edged and smoothed geons did not show any important difference. It suggests that the variation in the position of the apparent inner edges of the smoothed geons due to a light change did not prejudice the original object recognition (mean correct responses for smoothed geons under a modification of the light condition = 65.17%; mean correct responses after the same modification with the edged geons = 61.83%).

Experiments 1 and 2 both show that macaques trained with realistic illuminated geons, either edged or smoothed, revealed comparable above-chance performance to the line drawing and silhouette stimuli, confirming that information about the outline shape of the original represented object is sufficient to associate the modified object with the original. Results also confirm the important role of the internal surface information, as revealed by the transfer of performance obtained with the geons submitted to a change of the direction of the illumination. Taken together, these results largely favor Tarr and Pinker's (1990) viewer-based theory, and imply that lighting information is stored in the object representation for macaques.

Experiment 3

In this last experiment, we wanted to test whether macaques would be able to reconstruct the geon from new texture information, and whether this information could supply the specific surface cues, such as the shading information previously shown as critical in the macaques' representation of the object. Actually, it has been shown in the literature (for a review, see Todd, 2004) that one of the possible sources of visual information for the depiction of the 3D shape is a gradient of texture. Experiment 3 therefore trained the same five macaques, in the four-alternative forced-choice task, to discriminate four new original geons and tested them with the original geons filled with a new texture: a pattern of parallel lines or a pattern of dots. Our hypothesis was that if macaques do not mainly rely on edge-based representations as suggested by the first two experiments, then performance in the recognition of an object submitted to a radical modification of the surface cues, that is, a new texture, may be affected but not completely impaired.

Method

Stimuli—The stimuli used were two smoothed geons (an arch and a diabolo) and two edged geons (two prisms), as illustrated in Figure 1—Experiment 3, A, B, C, D (the diabolo, in fact, comprised two identical geons but was called “a geon”). As inferred from the viewing distance, their size varied from 11.4 to 14.4 visual degrees in width (i.e., 6.0 to 7.6 cm) and from 8.8 to 12.0 visual degrees in height (i.e., 4.6 to 6.3 cm). The total surface of each geon was, respectively, 18.9 cm², 18.7 cm², 22.6 cm², and 21.9 cm² for geons A, B, C, and D. The average grayscale for each geon was similar (147, 179, 158, and 170 for geons A, B, C, and D, respectively) according to the grayscale saturation that could range from 0 for white to 255 for black.

The test stimuli consisted of 3D objects rendered from the projection of elements on its surface: here a gradient of texture from a pattern of parallel surface contours and a gradient of texture from a pattern of dots (see Figure 1—Experiment 3, A', A'', C', C''). The average grayscale for these textured geons was not calculated because exactly the same patterns of texture (parallel lines or random dots) were applied for each test stimuli.

Procedure—After the training phase, the monkeys were given 15 test sessions, each consisting of 116 trials, including 100 differentially reinforced baseline trials (with the presentation of the four geon training stimuli) and 16 nonreinforced test trials. These 16 test trials correspond to two presentations of each test stimulus ($n = 8$ corresponding to the four geons and the two possible textures) within a single session.

Results

The monkeys required 71.2 sessions on average ($SEM = 17.2$) to reach the training criterion. They also performed well on the training stimuli in the test phase. Although the performance achieved with the test geons filled with new textures was lower than with the original geons (see Figure 6), the five monkeys were above chance (25%) in all the test conditions (see Table 3).

A one-way ANOVA conducted on the scores and considering the stimulus type (training geons, geons filled with lines, and geons filled with dots) showed that the performance depended on the stimulus type, $F(2, 8) = 73.04$, $p < .001$. A Tukey post hoc analysis indicated that the training stimuli were the best recognized ($ps < .001$) but did not reveal any significant difference between the two types of textured stimuli ($ps > .05$).

In addition, a comparison between the recognition performance obtained with the smoothed- and the edged-textured geons shows no reliable difference: one-way repeated ANOVA, $F(1, 4) = 4.51$, $p > .05$, in spite of a numerically large difference (mean smoothed-textured geons = 40.50%, $SEM = 8.69$; mean edged-textured geons = 60.67%, $SEM = 3.0$), suggesting that these test geons may have varied in the cues provided to the monkeys.

Discussion

This last experiment provides at least the demonstration that a radical change in the surface cues does not prevent object recognition. Geons filled with either new texture (parallel lines or dots) were recognized above chance by the macaques, but less well than the original geons. Thus, if the texture could have been processed to depict 3D shape of the object, it seems to be less efficient than the original shading information. Consequently, the more the surface cues share pictorial similarities with the original object, the more the object is readily recognized. Experiment 3 does not preclude the possibility that recognition of textured geons was driven by the silhouette or by internal information. Indeed, despite our efforts to design some various and rigorous stimuli, silhouette information is still present in all test stimuli, and a close examination of the smoothed-textured geons reveals that they did contain some remaining internal contours.

General Discussion

Taken together, the current findings indicate that shading information was the more salient cue used by macaques to store an object's representation in our experimental conditions. Our results also demonstrate that macaques have the adaptive ability to use some other cues to recognize an object, such as the outline shape. In conclusion, as predicted by a surface coding account, recognition performance of macaques benefits from the depiction of surface details, such as the texture and shading information. Next, we discuss our results considering the relevant literature on animal and human object recognition.

Recognition of a Line Drawing of an Object

Experiments 1 and 2 reveal a noteworthy positive transfer of performance to line drawing stimuli. Indeed, several studies in macaques and pigeons have shown that these animals failed to demonstrate a positive transfer from an original object to its line drawing (e.g., Tolan et al., 1981; Young et al., 2001; Peissig, Young, Wasserman, & Biederman, 2005). Thus far, there is only limited evidence for successful transfer to line drawings in non-human primates, and this concerned a very small number of subjects (e.g., Kovacs et al., 2003), few highly simple stimuli (e.g., Zimmermann & Hochberg, 1970), or language-trained chimpanzees (e.g., Hayes & Hayes, 1953; Itakura, 1994). We believe that our experiment overcomes the limitations of previous experiments by testing five macaques in the recognition of eight different rigorously designed objects, and thus provides two major conclusions. First, it now demonstrates that macaques are able to recognize and memorize the shape of a volumetric object by relying on the information yielded by the line drawing of that object. And second, behavioral data finally confirm electrophysiological results that show that shape-selective IT neurons remained selective for line drawings of objects (Kovacs et al., 2003).

Recognition of a Silhouette of an Object

Experiments 1 and 2 also demonstrate that macaques are able to recognize the original volumetric object (the geon) from its silhouette. This result is in agreement with a large behavioral literature (pigeons: e.g., Young et al., 2001; macaques: e.g., Tolan et al., 1981). It is also in accordance with neurophysiological studies showing that IT neurons are sensitive to the stimulus shape (e.g., Gross, Rocha-Miranda, & Bender, 1972; Desimone et al., 1984). Kovacs et al. (2003) recently reported that the presentation of a silhouette stimulus has only mild effects on the selectivity of the IT neurons.

In that context, our results establish that macaques undoubtedly use the outline contour of a represented object to memorize it, even when the inner contours of the object are available (e.g., for the line drawings). From an ecological point of view, one could expect that performance with the silhouette of the original object should be better than that with the line drawing. In the wild, animals may be confronted with an object placed in a backlit situation, thus creating the silhouette of an object, whereas they rarely have the opportunity to observe schematized line drawings. Absence of a difference between these conditions (silhouette and line drawing) could be explained by two possible assumptions. First, macaques may neglect the information of internal contours contained in the line drawings, especially in the case of

line drawings of smoothed geons, because they contained very few or even no inner contours. In that case, macaques focused their attention only on the outline shape of the object to memorize it. The second possibility is that the intensive prior experience of the macaques tested in that study with different kinds of pictorial representation, due to their long past history in laboratory testing conditions (e.g., Flemming, Beran, & Washburn, 2007), could have facilitated the recognition of degraded stimuli such as the line drawings.

Recognition of an Object Filled With New Surface Information

Macaques were able to recognize geons filled with a new texture and geons submitted to a modification of the light direction, creating some variations in the appearance of internal shadows and reflections, as well as some variations in the position of the apparent inner edges (smoothed geon condition). Our results suggest that an absolute surface pictorial similarity between two identical objects is not a prerequisite for above-chance object recognition. It is interesting that contrasting our results with those of Young et al. (2001) shows a major difference, although it leads to the same conclusion. They found that the silhouette and the light change stimuli were not differently recognized by pigeons. In our case, macaques performed similarly for line drawing and silhouette stimuli. Taken together, these findings suggest that the inner edges, present both in line drawing and in light change stimuli, exhibited no discriminative control for object recognition in both species. Consequently, the better performance for the light change stimuli in our study likely reflects the use of surface information more than the contribution of the edges. The fact that pictorial similarity with the original object actually favored object recognition can be explained by the “ecological” value of these stimuli. Indeed, the objects seen under a light change in our experimental conditions are close to those that would result from the changes of the position of objects relative to an artificial or natural light source or the diurnal and seasonal variations of natural light sources.

Our behavioral data are also in accordance with neurophysiological research that has specifically studied the selectivity of IT neurons to surface information. Liu, Vogels, and Orban (2004) showed that macaque IT neurons code for depth defined by texture gradients and invariantly over different types of texture. Weiskrantz and Saunders (1984) first showed that macaques with IT lesions were impaired in identifying a light-transformed object compared with its original version. They thus suggested that the original surface information is stored in the object's representation in macaques, and we behaviorally confirmed that assumption by the decline of recognition performance observed after a change in the illumination of objects. More recently, Vogels and Biederman (2002) recorded a constant activity of IT neurons while macaques were viewing objects illuminated from different directions. They concluded that IT is involved in the encoding of multiple views of a same object, authorizing a greater behavioral flexibility. That study also accounts for our own results, which revealed above-chance performance for objects submitted to a change in the light direction.

Conclusion

The current investigation was motivated by two major questions: Do monkeys have the ability to identify objects subjected to large variations in their visual appearance, in

experimental conditions, as it is required for an observer in everyday life? And then, what are the visual characteristics needed to succeed in such processing? Although our three experiments stressed the central role of the surface characteristics for object recognition in nonhuman primates, we are perfectly aware that our findings reflect a processing depending on the properties and the number of objects used within the experimental procedures. Indeed, one can hypothesize that the use of a restricted set of objects to train and test our monkeys could have favored the processing of one kind of information, that is, the surface information. However, many reasons encouraged us to limit our sample size. First, using a limited number of objects allowed us to control the effect of prior history in monkeys' performance (even if laboratory animals can rarely be considered as completely naïve). Second, most of the previous studies on object recognition and on picture perception that have used complex and realistic stimuli experienced difficulty isolating the cues that provide recognition. This difficulty generally leads to the conclusion that nonhuman primates rely on the combination of multiple cues, rather than on a single kind of information. For instance, Vogels (1999) demonstrated that monkeys' categorical discrimination of complex objects was not based on a single low-level feature, but rather on feature combinations such as color, form, and texture. It is interesting that our experiment, using artificial objects, also leads to the conclusion that monkeys have the flexible ability to use different cues depending on the nature and the complexity of the stimuli to be discriminated. Although our sample size was limited in each experiment (though larger than in previous studies), we note that our results were highly consistent across subjects, and across studies, in highlighting the contribution of surface cues. This consistency suggests that surface cues may also prevail during the recognition of a large number of different geons. Surface cues may be similarly important with more natural objects, but further investigation would obviously be necessary to clarify this during the recognition of more natural objects by nonhuman primates.

The present research, by contributing to an ongoing enterprise intended to determine which features of 2D renderings of 3D volumes are being used by monkeys, also allows us to draw a model of nonhuman primate object recognition comparable to the human model. On one hand, our results are in perfect line with human data that stress the role of surface cues in object recognition (e.g., Price & Humphreys, 1989; Tarr et al., 1998). On the other hand, our results diverge from the human studies that suggest that edge information alone, such as a line drawing (Biederman & Ju, 1988) or silhouette (Hayward et al., 1999) of an object, yields enough information for its normal recognition. Finally, it is suggested that object recognition could have possibly evolved; our findings have thus direct theoretical implications for the comparative study of object recognition.

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Figure 1.

Experiment 1: Representation of the four training edged geons A: a truss, B: a brick, C: a wedge, D: a prism. Some examples of the test stimuli: A': line drawing of the truss; A'': silhouette of the truss; A''', B''', C''', D''': the original edged geons seen under a change in the light direction. Experiment 2: Representation of the four training smoothed geons A: a pear, B: a barrel, C: a noodle, D: a cone. Some examples of the test stimuli: A': line drawing of the pear; A'': silhouette of the pear; A''', B''', C''', D''': the original smoothed geons seen under a change in the light direction. Experiment 3: Representation of the four training geons. A: an arch (smoothed geon), B: a diabolo (smoothed geon), C and D: two different prisms (edged geons). Some examples of the test stimuli: A': the arch rendered with a pattern of dots, A'': the arch rendered with a pattern of parallel lines, C': the prism rendered with a pattern of dots, C'': the prism rendered with a pattern of parallel lines.

Figure 2.

Mean percentage of correct responses (with standard error bars) for each stimulus type for the test phase of Experiment 1.

Figure 3.

(A) Mean percentage of correct responses (with standard error bars) for the first and the second test trials of Experiment 1, averaged for the five monkeys, the 12 test stimuli, and the 15 test sessions. (B) Mean percentage of correct responses (with standard error bars) across the 15 test trials of Experiment 1, averaged for the two test trials, the 12 test stimuli, and the five monkeys.

Figure 4.

Mean percentage of correct responses (with standard error bars) for each stimulus type for the test phase of Experiment 2.

Figure 5.

(A) Mean percentage of correct responses (with standard error bars) for the first and the second test trials, averaged for the five monkeys, the 12 test stimuli, and the 15 test sessions of Experiment 2. (B) Mean percentage of correct responses (with standard error bars) across the 15 test trials of Experiment 2, averaged for the two test trials, the 12 test stimuli, and the five monkeys.

Figure 6.
Mean percentage of correct responses (with standard error bars) for each stimulus type for the test phase of Experiment 3.

Table 1
Individual Results of the Test Phase of Experiment 1 for Five Macaques in Each Test Condition: Line Drawing, Silhouette, and Change in Light Direction

Experiment 1	Line drawing	Silhouette	Light change
Monkey 1	CR = 44.17%	CR = 46.67%	CR = 58.33%
	S = 53	S = 56	S = 70
	$z = 4.85; p < .001$	$z = 5.48; p < .001$	$z = 8.43; p < .001$
Monkey 2	CR = 50.00%	CR = 48.33%	CR = 62.50%
	S = 60	S = 58	S = 75
	$z = 6.32; p < .001$	$z = 5.90; p < .001$	$z = 9.49; p < .001$
Monkey 3	CR = 39.17%	CR = 45.00%	CR = 67.50%
	S = 47	S = 54	S = 81
	$z = 3.58; p < .001$	$z = 5.06; p < .001$	$z = 10.75; p < .001$
Monkey 4	CR = 34.17%	CR = 61.67%	CR = 64.17%
	S = 41	S = 74	S = 77
	$z = 2.31; p < .001$	$z = 9.27; p < .001$	$z = 9.91; p < .001$
Monkey 5	CR = 35.83%	CR = 41.67%	CR = 56.67%
	S = 43	S = 50	S = 68
	$z = 2.74; p < .001$	$z = 4.21; p < .001$	$z = 8.01; p < .001$

Note. CR = mean percentage of correct responses; S = score defined as the total number of correct responses over 120 total trials; z = results of the one-tailed individual binomial test.

Table 2
Individual Results of the Test Phase of Experiment 2 for Five Macaques in Each Test Condition: Line Drawing, Silhouette, and Change in Light Direction

Experiment 2	Line drawing	Silhouette	Light change
Monkey 1	CR = 50.00%	CR = 56.67%	CR = 61.67%
	S = 60	S = 68	S = 74
	$z = 6.32; p < .001$	$z = 8.01; p < .001$	$z = 9.27; p < .001$
Monkey 2	CR = 46.67%	CR = 52.50%	CR = 57.50%
	S = 56	S = 63	S = 63
	$z = 5.48; p < .001$	$z = 6.96; p < .001$	$z = 8.22; p < .001$
Monkey 3	CR = 51.67%	CR = 38.33%	CR = 70.00%
	S = 62	S = 46	S = 84
	$z = 6.74; p < .001$	$z = 3.37; p < .001$	$z = 11.38; p < .001$
Monkey 4	CR = 34.17%	CR = 63.33%	CR = 71.67%
	S = 41	S = 76	S = 86
	$z = 2.32; p < .001$	$z = 9.7; p < .001$	$z = 11.81; p < .001$
Monkey 5	CR = 55.00%	CR = 45.00%	CR = 65.00%
	S = 66	S = 54	S = 78
	$z = 7.59; p < .001$	$z = 5.06; p < .001$	$z = 10.12; p < .001$

Note. CR = mean percentage of correct responses; S = score defined as the total number of correct responses over 120 total trials; z = results of the one-tailed individual binomial test.

Table 3
Individual Results of the Test Phase of Experiment 3 for Five Macaques in Each Test
Condition: Parallel Lines and Random Dots

Experiment 3	Parallel lines	Random dots
Monkey 1	CR = 60.83%	CR = 47.50%
	S = 73	S = 57
	$z = 9.06; p < .001$	$z = 5.69; p < .001$
Monkey 2	CR = 53.33%	CR = 60.00%
	S = 64	S = 72
	$z = 7.17; p < .001$	$z = 8.85; p < .001$
Monkey 3	CR = 37.50%	CR = 44.17%
	S = 45	S = 53
	$z = 3.16; p < .001$	$z = 4.85; p < .001$
Monkey 4	CR = 58.33%	CR = 54.17%
	S = 70	S = 65
	$z = 8.43; p < .001$	$z = 7.38; p < .001$
Monkey 5	CR = 41.67%	CR = 40.00%
	S = 50	S = 48
	$z = 4.21; p < .001$	$z = 3.79; p < .001$

Note. CR = mean percentage of correct responses; S = score defined as the total number of correct responses over 120 total trials; z = results of the one-tailed individual binomial test.