Mouse ability to perceive subjective contours

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1. Abstract

In contrast to the previously held notion that mice have a weak visual system, it is now generally accepted that mice can perceive rather complicated figures in various contexts such as in cognitive experiments and in social settings. Here, we show that mice could even be capable of perceiving a visual illusion—subjective contours. This illusion requires the visual system to compensate for a lack of visual information in compressed 2D images on the retina. In this experiment, we trained mice to respond appropriately to a

rectangle-shaped rewarded figure of specific orientation in a two-choice visual discrimination task with a touchscreen monitor. In transfer test 1, mice could discriminate illusory rectangle-shaped figures significantly as compared to a figure, which did not induce illusory figures. In transfer test 2, the choice rate of targets decreased with imperfect illusory figures, which produced weak perception of rotated or deficient inducers. Moreover, in transfer test 3, mice could not discriminate the low-resolution illusory figure, which also induced weak perception. These results demonstrated the possibility that mice might be useful for investigating fundamental properties of the neural visual system.

1. Introduction

Visual perception is the ability to interpret the surrounding environment by processing visual cues. The visual cortex of vertebrates receives input from the eyes, and then analyzes and modifies this visual information. In order to perceive an object, it is important to be able to supplement visual cues in situations where such information might be lacking. For example, the reconstruction of absent contours due to their partial occlusion is essential for an animal's survival in the wild; the animal would be at higher risk of dying if it stalled in identifying an object as a predator or as food. The ability to perceive subjective contours (SCs) is one mechanism used to find obscure outlines from physical counterparts.

The Kanizsa triangle is frequently used to induce perception of SCs [1]. The triangle-illusion is created by the arrangement of three inducers, such as "Pacman" figures, positioned with their open angles all pointing inward. Other types of SCs are defined by grating gaps and phase-shifting abutting gratings. The Kanizsa triangle induces not only SCs, but also illusory brightness and depth. Several studies have used SCs to investigate the ability of animals to complement visual information. These studies have reported that humans and several other animal species can perceive SCs [2], including Macaque monkeys [3], cats [4], birds [5, 6], fish [7, 8], and even insects [9]. Taken together, the findings of these reports suggest that the ability to perceive SCs may have been acquired early in evolution [10]. However, it is still not clear if mice have the ability to perceive SCs. The laboratory mouse is one of the most popular mammalian models used to clarify activity of the neural networks that underlie cognition and perception at the single cell level. The

activity of these networks can be evaluated using a variety of approaches such as genetic technologies, electrophysiological measurements, behavior analysis, and so on. We therefore examined whether mice could perceive SCs using a touchscreen system, which is a powerful tool for visual associative learning in a two-choice visual discrimination task. We used figures such as lacking or rotating inducers to exclude the possibility of providing mice with discrimination clues from local features. Previous experiments in humans have determined that SCs perception decreases with weakening resolution [11]. Therefore, in the last experiment we blurred edges of SC figures with a Gaussian filter to determine whether choice rate was affected in mice. We hypothesized that if the discrimination rate of each mouse was reduced following this manipulation, it would suggest that clear salient inducer regions are essential to distinguish figures.

2. Materials and methods

2.1. Animals

Ten male mice were used for the experiments (BDF_1; Japan SLC Inc., Shizuoka, Japan). Mice were housed and trained in a temperature (23–24°C) and humidity (50–70%) controlled room under a 12 h light/dark cycle. All experiments were carried out during the light phase. All procedures were conducted with approval from, and in strict compliance with, the animal welfare policies of the Institutional Animal Care and Use Committee of Nara Institute of Science and Technology. All efforts were made to minimize animal suffering.

2.2. Apparatus

Preliminary training and testing were carried out with a customized touchscreen testing chamber (Fig. 1A). We referred to Morton et al. for building this system [12]. The operant chamber for mouse (30.5 × 24.1 × 8.25 cm, Knosys Olfactometers Inc., Florida, USA) was modified with clear Perspex walls and a food magazine. The food magazine held a dispenser (Muromachi Kikai Co. Ltd., Tokyo, Japan) for mouse pellets (F05684, Bio serv, Inc., New Jersey, USA), a magazine light, a click sound device, and a photocell sensor to detect nose-poke activity. A house light (3 W) and tone generator were set on the ceiling of the chamber and a touchscreen was set on the opposite side of the food magazine. The touchscreen consisted of a flat-screen monitor (3.5 inch; Castrade Co., Ltd., Tokyo, Japan) equipped with an infrared- arrayed touch sensor (Nitto denko Co., Osaka, Japan). The

touchscreen was covered with two response windows (35 × 50 mm, 20 mm from the floor) using a black Perspex plate. A plastic stick was attached to the plate under the response windows in order to avoid unwanted touching (e.g. tail, body). Computerized visual stimuli were displayed in the area of each window and controlled by LabVIEW (National Instruments Japan Corp., Tokyo, Japan).

2.3. Visual discrimination and test procedure

2.3.1. General procedures

Mice underwent behavioral test at 8 weeks of age and trained 5–6 days/week in the same chamber. Pre-training, training, and transfer tests lasted for 60 min or until mice reached a set of pre-determined criteria. For example, in the pre-training phase, mice had to perform particular actions (details described below) in order for us to confirm that habituation to the experimental apparatus had occurred. In the training phase, we also set criteria for visual discrimination in which mice had to successfully complete two consecutive sessions with 80% correct choices within 20 trials. Finally, in the testing phase, the criterion for presenting the test figure was that mice had to succeed in visual discrimination with a rate of over 80%. During experiments, mice were fed a restricted diet to maintain body weight to at least 85% of predicted free feeding. Water was available ad libitum.

2.3.2. Pre-training

In the pre-training phase, we used the arranged touchscreen-based operant procedure for mice [13]. Pre-training consisted of an acclimatization stage, which was then followed by

four subsequent stages. In the acclimation stage, 10 pellets were supplied beforehand in the magazine and the magazine light was always illuminated. When mice took all pellets within 20 min, pre-training proceeded to the next stage. In the first stage, a figure was presented on only one side of the windows. The figure was comprised of several types of shapes on a black background, and it was randomly selected and presented over the right or left window (the inactive window had no figure). Mice were required to touch their noses to the window that presented the figure, after which the screen immediately changed to a gray background. At the same time, a pellet was supplied, a tone was presented for 1 s, and the magazine light was illuminated for 3 s to announce the existence of a food pellet. If mice touched the window that did not present the figure, the screen was changed to gray and mice were supplied a pellet after a 15 s delay. In the second stage, rewards were only given when mice correctly chose the window that presented the figure. In the third stage, mice were required to poke the food magazine with their snouts to initiate a trial. When the trial started, the magazine light was turned on. Next, when mice poked their noses into the food magazine, a clicking sound was played. Mice then pulled their noses out of the food magazine, the light was turned off, and the figure appeared on the screen. When mice selected the black window in the final stage, the house light was turned on for 5 s and the termination of the trial was delayed for 5 s more to inform the mouse of their incorrect choice as punishment. In the first to third stages, mice were approved to proceed to the next stage when they collected 30 rewards (trials) in 60 min. In the fourth stage, the criterion was met when mice selected the window that presented the figure more than 23 out of 30 trials. Moreover, mice

had to succeed over two consecutive sessions. During all stages, the inter-trial interval (ITI) was 15 s.

2.3.3. Training

Once mice had completed the pre-training phase, they were trained on a two-choice visual discrimination task using a rectangle-shaped figure (bar) of vertical and horizontal orientation. Mice were classified into two groups: “Vertical group” where a vertical bar was set as the correct stimulus (S+) and a horizontal bar as the incorrect stimulus (S-), and “Horizontal group” with a horizontal bar as S+ and a vertical bar as S-. Each session consisted of a maximum of 40 trials and the ITI was 10 s. Following trial initiation, a pair of stimuli would appear on the windows: one S+ and the other S-. When a mouse selected S+, it was rewarded with a pellet, a tone, and a magazine light (similar to what mice encountered during the pre-training phase). On the other hand, when a mouse selected S-, it was forced to experience a 5 s time-out period. The same trial was repeated until it had been successfully completed (correction trial). The left–right arrangement of the stimuli was determined pseudo-randomly across trials. Training consisted of four stages with “bar-only,” “bar and non-inducers”, “non-inducers and inducers including a bar inside,” “both black and white backgrounds of the same figure in stage 3.” Those figures were prepared to normalize the luminous bias and figure-and-background contrast. Finally, all stimuli were novel to the animals at the start of the two-choice visual discrimination training and did not resemble any of the stimuli used in the pre-training stages. During all

stages, mice reached the criterion when they succeeded in two consecutive sessions with an accuracy of 80% (calculated using non-correction trials per session).

2.3.4. Transfer test 1 – Kanizsa illusion

After mice had reached criteria, we performed the transfer test using an SC figure forming the illusory bar with two inducers (Fig. 1C). To achieve similar luminosity between S+ and S- figures, we placed two additional "non-inducers" (these orientations differed from training figures to avoid a leaned spurious correlation) on the screen. One session consisted of 10−14 trials of visual discrimination with rewarded figures, which used the same figures in Stage 4, and one test trial with unrewarded figures (Fig. 1E). When the correct rate of trials exceeded 80% of the final trials, a pair of SC figures was shown once. No reward and no signal were supplied regardless of a mouse's reaction. Additionally, we also used nSC figures that did not induce subjective contours (Fig. 1D). Inducers of nSC figures were rotated 45, 90, 135, 180, 225, 270, and 315° clockwise to prevent the perception of the SCs bar (Fig. 1F). The session was conducted in the same manner as using SC figures. All transfer tests were carried out for 1 h/day, and we measured 20 choices/mouse. If a mouse did not pass less than two test sessions/day, we removed its data from the following appropriate test.

2.3.5. Transfer test 2 – Local features

To test whether mice could recognize illusory figures using local features or not, we used two types of figures: "Lack" had one inducer deleted (Fig. 2B, Left) and "Rot" had one

inducer rotated 45° clockwise (Fig. 2B, Right). These tests were performed in the same manner as transfer test 1.

2.3.6. Transfer test 3 – Filtering Kanizsa

Two types of modified SC figures were used: a low Gaussian filter (LGF, $\sigma = 5.0$) and a high Gaussian filter (HGF, $\sigma = 9.6$) using GIMP 2 (GNU Image Manipulation Program, GIMP Development Team, http://www.gimp.org/).

2.4. Statistical analysis

All data are expressed as group means ± SEM. Statistical comparisons of visual discrimination ability were performed by Student's *t* test for two group comparisons and Dunnett's test for multiple comparisons among more than two groups against the single control group (nSC). All data were analyzed with R (R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/).

3. Results

3.1. Mice distinguished between two forms of Kanizsa bars

In previous studies showed that animals significantly varies their behavior with an SC versus a control figure [7, 10]. Based on the assumption that operant conditioning via the automatic touchscreen system is effective, the aim of this study was to investigate whether mice had the ability to perceive SCs.

Two groups (vertical and horizontal) were used in Stage 1 training, and each group was composed of five mice. No significant difference was noted in the number of sessions that each group required to reach the criteria. As determined by a student's *t* test, the vertical group required 8.6 ± 1.2 sessions and the horizontal group required 8.4 ± 1.2 sessions ($p = .91$, Fig. 2A). From this result, we pooled both data together. During transfer test 1, we presented stimuli where one bar gave rise to an SCs while the other did not. Importantly, both stimuli were very similar to each other in terms of luminosity distribution because non-inducers were set and mice remained unrewarded regardless of their reactions. Figure 2C shows the mean values of choice rates made by 10 mice over 20 tests. The choice rate of discrimination with SCs was 73.0 ± 2.5%; however, nSC dropped to 47.5 ± 3.1%. This nSC rate was similar to random choice since a 50% discrimination rate indicated that mice were unable to discriminate between two figures. By comparing the choice rate of SC and nSC, it was obvious that a significant difference was acquired by Dunnett's test ($p < .001$).

3.2. Mice paid attention to entire figures, not just local features

It has been shown that the perception of Kanizsa figures can be abolished by the rearrangement of inducers. Previous studies have revealed that goldfish choice rate decreases when inducers are rotated and lack either upper or bottom parts of Kanizsa triangles and squares [7]. In our study, we used two types of figures: Lack and Rot. Fig. 2C shows that the choice rates of Lack and Rot were 44.0 ± 3.9% and 59.5 ± 3.5%, respectively. The choice rate for Lack exhibited no significance (p = .80), but the rate for Rot was significantly better compared with nSC by Dunnett's test (p = .03).

We also compared choice rate with the distribution of inducers in figures. Previously, it was shown that rats could differentiate triangular shapes from squares when the bottom portions of the figures are occluded [14]. This report suggests that mice can discriminate bar shapes by looking at inducer parts. Therefore, we predicted the choice rate of Lack and Rot would also vary depending on inducer locations. In order to examine this, we presented mice with figures where the bar shape could be identified by looking at either upper or lower parts of the figure at the same time. These results were then compared between nSC and both upper and lower presentation situations. As a result, choice rates of upper and lower regions of Lack were not significantly different from nSC. In contrast, Rot figures elicited significantly increased choice rates, whether appropriate inducers existed in the upper portion of the figure or not. These findings are consistent with results obtained by Wyzisk & Neumeyer [7]. However, it should be noted that in the Rot data, the presence of an inducer, even one that was not in the correct orientation, might have affected visual perception.

3.3. Choice rate decreased with weakened figure resolution

Figure 3B shows the choice rate made by nine mice for each figure (Vertical group n = 5, Horizontal group n = 4). One mouse was removed from Transfer test 3 because he did not achieve the criteria. The mean choice rates of nSC and SC were 46.7 ± 3.1% and 72.2 ± 2.5%, respectively. LGF was 62.8 ± 3.6% and showed significant differences between LGF and nSC (p = .003). On the other hand, HGF was 57.2 ± 3.0%, showing no significant differences between HGF and nSC by Dunnett's test (p = .06).

4. Discussion

In this study, we investigated the ability of mice to perceive SCs. We first examined the arrangement of each component in the figure used to induce SCs. Then, we measured the average discrimination rate for multiple control and SC figures in order to evaluate SCs perception in mice.

4.1. Mice were able to perceive subjective contours

As a result of the Kanizsa-type SC experiment, a significant difference was observed between the average discrimination rate of SC and nSC figures (Fig. 2C). The discrimination rate of SC figures indicated whether mice perceived similarities in bar shapes that they had learned beforehand. Using this assessment measure, we confirmed that the recognition rate of a figure that had been learned during training was over 80%. In addition, we observed a 7% decrease in SCs perception, even if mice showed 80% accuracy during the bar shape discrimination task. This reduction might have occurred because mice knew that they would not receive a reward with SC and control figures during the test phase that differed from training figures, thus resulting in a slight decrease in motivation. In fact, this decrease in discrimination has also been observed in previous studies, even in one study that used subjective contours to induce shape perception in goldfish; they observed an 8% decrease [7].

On the other hand, mice were not able to distinguish the orientation of the bar in the nSC figure. This finding was consistent with the discrimination rate for random selection in nSC

where inducer angles differed from angles in the SC figure. Therefore, we concluded that mice were able to perceive the bar shape in the SC figure, and that this represented the basic learned shape. This data also suggests that, like humans, mice are able to perceive SCs.

In the current study, we hypothesized that the high rate of discrimination was most likely influenced by local features. Therefore, we compared the average discrimination rate in the same mice using Lack and Rot figures in which one of the inducers was either absent or rotated, respectively. If mice made a selection taking only one of the inducers into account, the discrimination rate of Lack and Rot would be higher than 50%. On the other hand, it was thought that if mice perceived the bar shape from both inducers, the discrimination rate of Rot would be higher than Lack. As a result, when the Lack figure was presented, even though the angle of the inducer correctly configured the bar form (positive inducer), the discrimination rate was equivalent to the nSC condition where SCs was not induced. In contrast to the Lack figure, the position of the inducer seemed to have no influence on discrimination rates. Taken together, these results suggest that when one of the inducers was missing from the figure, even if the positive inducer was still presented, mice could not perceive similarities to the previously learned shape.

4.2. Perception was prevented following a decrease in edge contrast

Previous studies using visual illusions have indicated that the presentation of sharp edges is important in inducing subjective contours [15, 16]. In this study, we reduced the contrast of figure edges by applying a smoothing Gaussian filter. Although mice could move freely

to distinguish figures, we found that the average discrimination rate significantly dropped in the weakened edge condition (Fig. 3B). These results indicated the mice could still see the presented figure through the filter, even though they had weak visual ability. We presumed this was the case because mice were still able to move freely to distinguish figures, which suggesting that figure contrast is one of the most important factors needed to perceive SCs.

4.3. Visual learning in various mouse strains

In this study, we used BDF_1 mice; the F1 generation of a DBA/2J male and C57BL/6 female. The black coat of these mice was the same as the C57BL/6 mice, but BDF_1 mice were heavier in body weight and had longer lifespans than their inbred parents. In addition, it has been suggested that BDF_1 mice have superior environmental adaptability when compared to their inbred parents [17]. A previous study indicated that BDF_1 mice also exhibit greater visual perception in the radial maze task compared to both inbred strains [18].

In this experiment, no significant difference was found in the number of days that 13 C57BL/6 and 22 BDF_1 mice required for bar-shape discrimination (data not shown). This result indicates that C57BL/6 had similar visual ability to BDF_1 mice. Future studies will be able to elucidate the mechanisms that underlie higher-order visual perception using various biological and behavioral resources, such as genetically modified animals and behavioral apparatuses.

4.4. Visual perception in rodents compared with other species

Previous electrophysiological experiments in the macaque monkey have shown that neurons that respond to SCs are located in higher-order visual cortices, V1/V2 and V4. Moreover, in anesthetized monkeys, two-photon calcium imaging has revealed that information regarding direction is detected by neurons with small receptive fields in V1/V2 areas. This information is integrated before reaching cells with big receptive fields in V4 to detect broad SCs information [19]. However, the local circuit of neurons and the minimum number of responses required to form SCs perception have not yet been elucidated. In order to accomplish this, one would have to observe the perception of a behaving subject while measuring the correlation of neuronal activity at the single cell level. Simultaneous observation of activity in the cortical region would also be necessary to clarify the neural mechanisms of information transmission between cortical layers or between regions of the visual cortex in vivo. Furthermore, it would be necessary to perform these experiments in awake subjects in order to correspond neural activity to the perceptual magnitude of SCs.

Studies about the perception and cognition of rodents are more popular than ever. Mice have been used for genetic research, in which the introduction of a specific gene can produce transgenic mice, and optical approaches have become easier to apply to biological phenomena, such as flavoprotein fluorescence imaging, calcium imaging using two-photon microscopy [20,21], and the two-photon targeted patching method [22]. In addition, optogenetics has helped us to enhance or suppress activity of neurons at high spatial-temporal resolution by expressing channel rhodopsin or halo rhodopsin in a cell

membrane of interest [23−25]. Some similarities of neural mechanisms and structures have been found amongst large mammals. For example, the cat and monkey both have functional columnar structures in the visual cortex where populations of neurons respond to vertical or horizontal orientations. The visual resolution of the mouse is inferior compared with primates [26], but it has been found that mice also have a functional cluster in layer V of the visual cortex that is thought to be similar to the structure known as "column" in animals that have high visual acuity. This suggests that small neuronal circuits are present even in the mouse brain, and that these mediate perception similar to other animals [27]. Regarding neural mechanisms, it has been found that cats and monkeys have nearly identical orientation selectivity widths, and that the formation of their receptive fields and stimulus detection mechanisms are similar [28, 29].

Previous studies have found that rats have various visual ability. For example, the visual search ability of rats is able to overcome changes in shape information [12, 30]. Rats and mice also have the amodal completion ability, which involves integrating and complementing visual information from objects that are partially occluded [31, 32]. These data support our hypothesis. Moreover, a touchscreen system allows us to investigate the detailed process of visual perception and carry out more robust visual learning. Taken together, these studies all suggest that pairing rodent studies with various technologies, such as electrical devices, genetics, neurophysiology, and behavioral measurements, will help us to clarify the basic mechanisms of visual perception [33].

In this study, we found that mice were able to discriminate between distinct shapes induce SCs. Our findings will help to elucidate higher brain functioning in mice and will aid in our understanding of the precise mechanisms that are utilized by the visual system.

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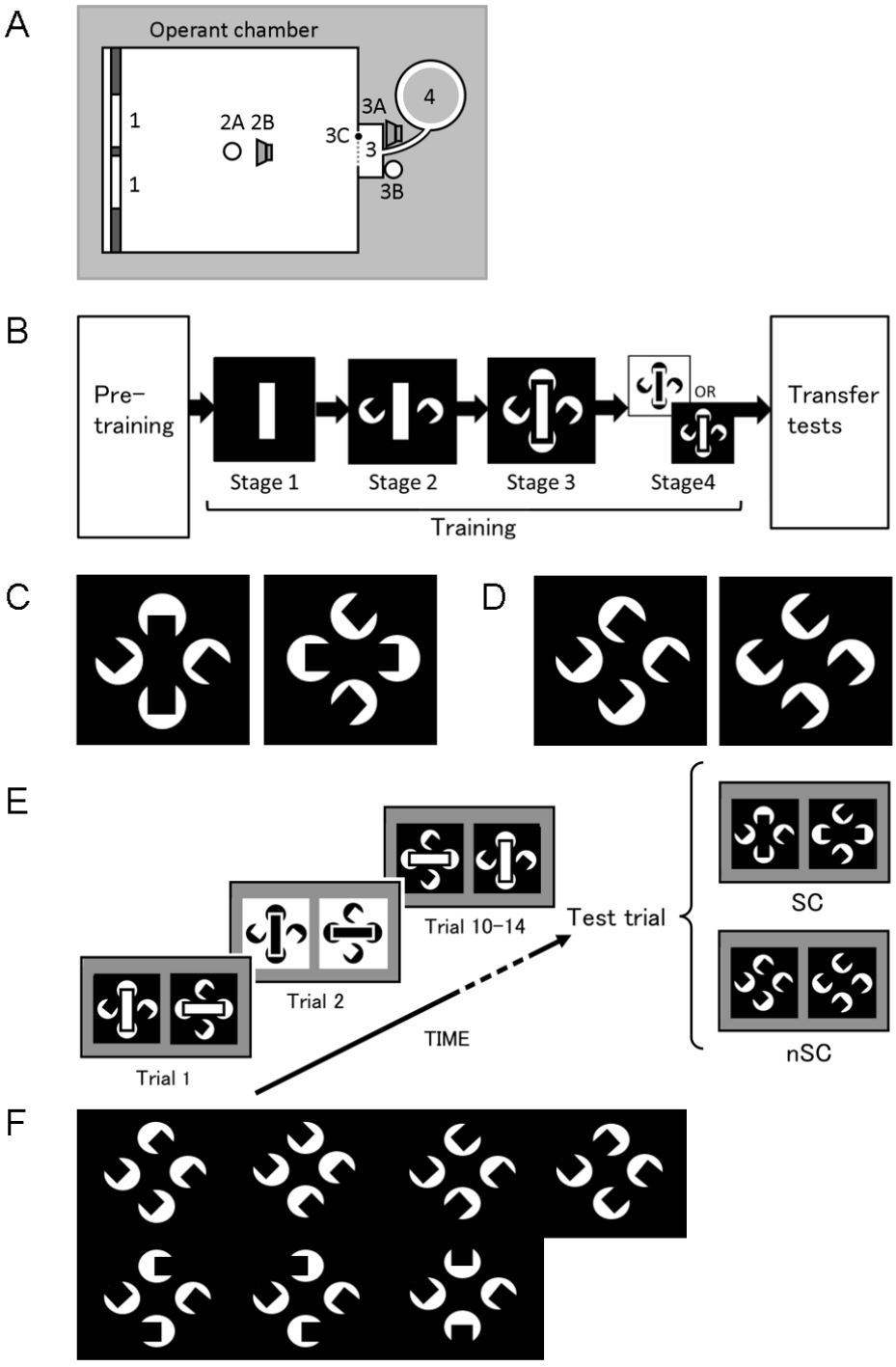
Figure Legends

Fig. 1 The apparatus and task procedure.

A, Schematic image of the operant chamber (overhead view). 1: windows, 2A: house light, 2B: sound generator, 2A and 2B attached on the chamber roof. 3: food magazine, 3A: click sound device, 3B: magazine light, 3C: photocell sensor, 4: food dispenser connected to the magazine with a tube. B, The common schedule from pre-training to transfer tests. This consisted of pre-training, four training stages, and a transfer test. In the training stages (stages 1−4), mice learned how to correctly discriminate between vertical or horizontal bar shapes, one of which was reinforced. In the final stage (stage 4), we provided both black and white background figures to categorize the bar shape itself. C, Visual stimuli used in transfer test 1 as SC figures. Vertical and horizontal figures are indicated on the left and right, respectively. D, Visual stimuli used in transfer test 1 as nSC figures. Vertical and horizontal figures are indicated on the left and right, respectively. E, Schedule of the transfer test trial. F, Seven types of visual stimuli were used in the transfer test as vertical-type nSC figures. These stimuli were contented the same inducers as SCs, but did not induce perception of subjective contours.


A
Operant chamber
1
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Pre-
training
Stage 1
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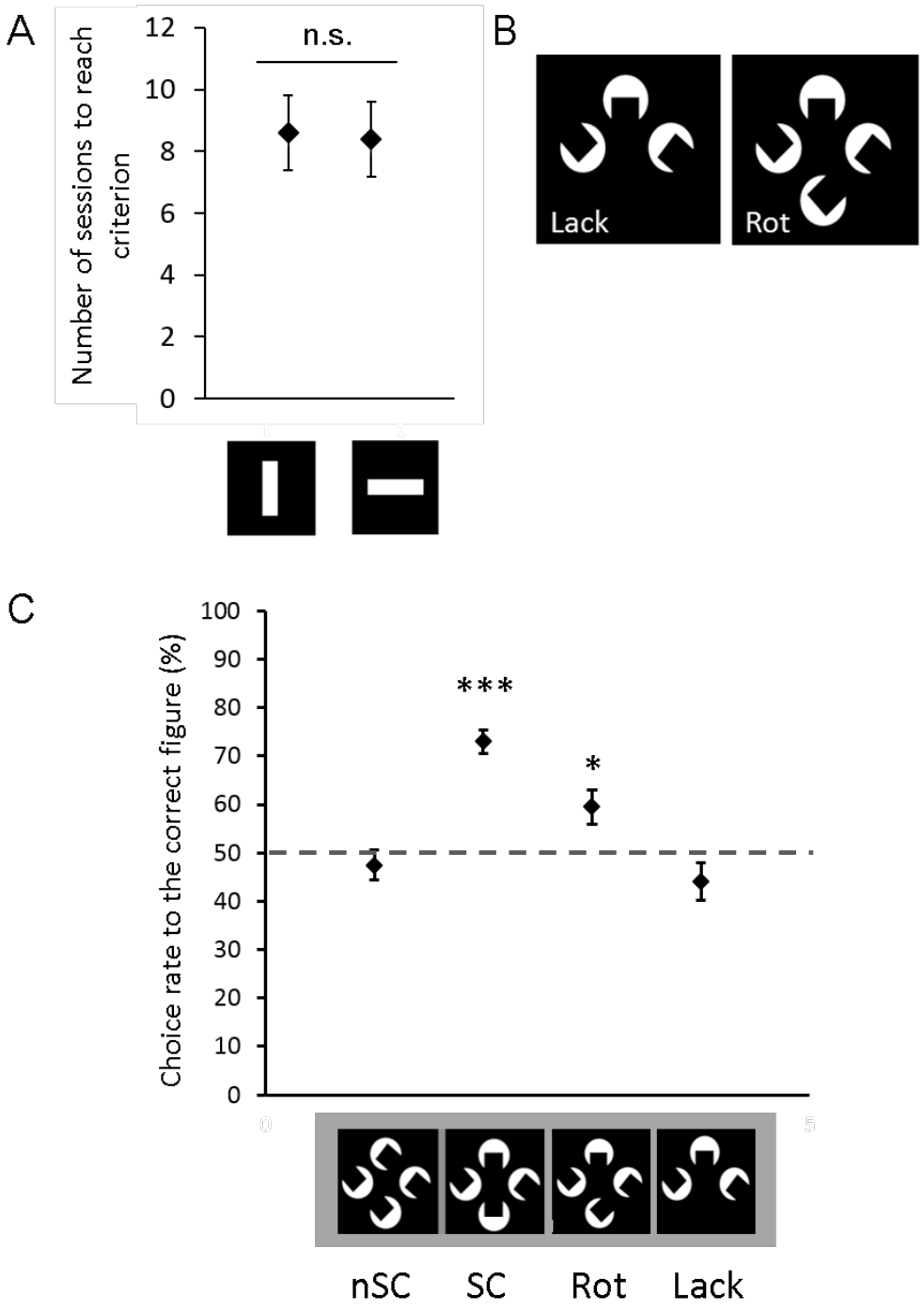
OR
Stage4
Transfer
tests
Training
C
D
E
Trial 1
Trial 2
Trial 10-14
Test trial
TIME
SC
nSC
F

Fig. 2 Inducers of SCs affected discrimination performance in mice.

A, Number of sessions required to reach criterion in training Stage 1. Ten mice were equally classified into two groups. Vertical group: the vertical bar is S+ and the horizontal bar is S- . Horizontal group: the vertical bar is S- and the horizontal bar is S+. Data are shown as mean ± SEM. n.s. not significant (student's *t* test) B, Visual stimuli used in transfer test 2. Lack was a figure that was devoid of one inducer and Rot was a figure in which one of the inducers was rotated to decrease the perception of subjective contours. C, The rates of ideal correct figure selections in each test. The dashed line shows the random choice rate, which was 50%. All data are shown as mean ± SEM. * $p < .05$, *** $p < .001$ (Dunnett's test)


A
Number of sessions to reach criterion
12
10
8
6
4
2
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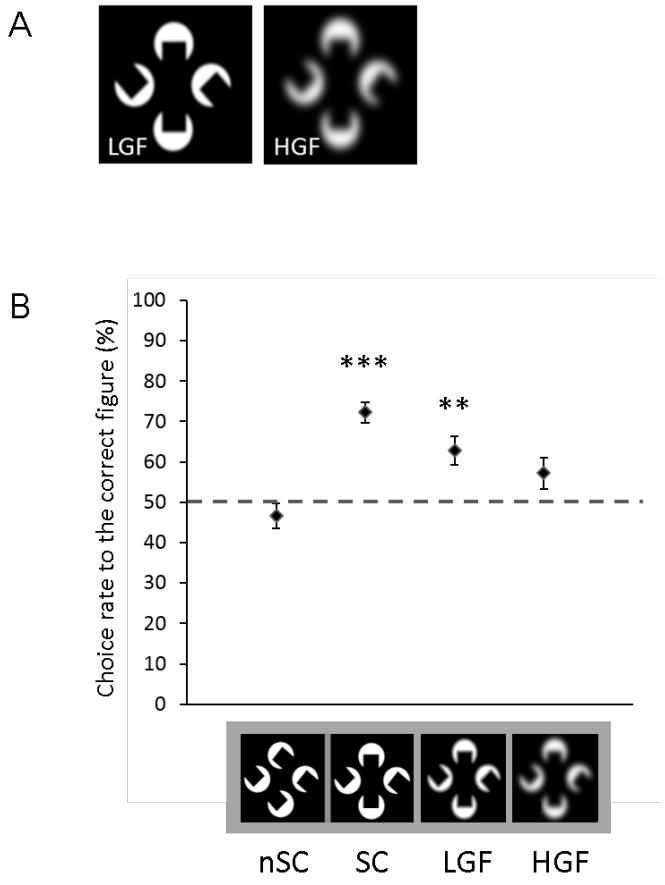
n.s.
B
Lack
Rot
C
Choice rate to the correct figure (%)
100
90
80
70
60
50
40
30
20
10
0
***
*
nSC
SC
Rot
Lack

Fig.3 Perception of SCs was prevented following a decrease in the contrast of figure edges. A, Visual stimuli used in transfer test 3. All stimuli show the same type of figure; the vertical figure, for instance. Low Gaussian filter (LGF) and high Gaussian filter (HGF) indicate figures with low and high fuzzy boundaries, respectively.

B, Ideal selection rate of correct figures in each trial. All data are shown as mean ± SEM. ** $p < .01$, *** $p < .001$ (Dunnett's test)



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