



Category learning in rodents using touchscreen-based tasks

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Data Availability Statement

The data for the rat and human tasks are openly available in Dryad at:

<https://doi.org/10.5061/dryad.qv9s4mwbm>. Codes for the tasks and a list of hardware for the touchscreen apparatus are available at:

<https://github.com/FreemanlabUIowa/RodentCategorization>.

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Abstract

Categorization is a fundamental cognitive function that organizes our experiences into meaningful 'chunks.' This category knowledge can then be generalized to novel stimuli and situations. Multiple clinical populations, including people with Parkinson's disease, amnesia, autism, ADHD, and schizophrenia, have impairments in the acquisition and use of categories. Although rodent research is well suited for examining the neural mechanisms underlying cognitive functions, many rodent cognitive tasks have limited translational value. To bridge this gap, we use touchscreens to permit greater flexibility in stimulus presentation and task design, track key dependent measures, and minimize experimenter involvement. Touchscreens offer a valuable tool for creating rodent cognitive tasks that are directly comparable to tasks used with humans. Touchscreen tasks are also readily used with cutting-edge neuroscientific methods that are difficult to do in humans such as optogenetics, chemogenetics, neurophysiology, and calcium imaging (using miniscopes). In this review, we demonstrate advantages of touchscreen-based tasks for studying category learning in rats. We also address multiple factors for consideration when designing category learning tasks, including the limitations of the rodent visual system, experimental design, and analysis strategies.

Keywords

Rat, visual category learning, touchscreen, translational research, executive function, selective attention, category generalization

1 INTRODUCTION

Categorization allows for the organization of stimuli, ideas, and events into meaningful ‘chunks.’¹⁻⁴ Organizing information in such a way makes encoding and representing stimuli more efficient, as only information relevant to the category is necessary, and allows for immediate generalization to novel situations.⁵⁻⁷ Learning a new category involves multiple cognitive functions, including attention, working memory, long-term memory, and decision making, and therefore requires complex interactions among multiple brain regions.⁸⁻¹⁵

Several clinical populations exhibit deficits in category learning, which are presumably caused by pathology in the neural systems underlying categorization. For example, patients with Parkinson’s disease, who have impaired basal ganglia function, are typically impaired on category learning tasks that require combining information from multiple stimulus dimensions, such as information integration (II) tasks and weather prediction tasks.¹⁶⁻¹⁹ Patients with Huntington’s disease, ADHD, autism, and schizophrenia are also impaired on these tasks.²⁰⁻²³ To learn category structures that can be solved by a single category dimension (e.g., rule-based tasks; RB), humans often develop and test verbalizable category rules.²⁴ Patients with disorders that affect hippocampus functioning, including amnesia and Alzheimer’s disease, are typically impaired to learn RB tasks.²⁵⁻²⁶ Parkinson’s patients are also impaired on RB tasks, which has been attributed to a reduced ability to maintain the current rule across trials.²⁷ Although the impairments in category learning in these populations can generally be related to neurological

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deficits, the specific causes of their deficits remain elusive because the neural mechanisms underlying category learning are largely unknown. Therefore, there is a critical need for a systematic analysis of the neural mechanisms underlying category learning using animal models.

Rodents are well suited for determining the neural mechanisms underlying cognitive functions, and although the study of categorization in non-human animals has heavily relied on pigeons,²⁸⁻³⁴ rats are capable of category learning.³⁵⁻⁴² We have developed category learning tasks for rats using touchscreens as a foundation for a systematic analysis of the neural mechanisms underlying categorization. The advantages of this methodology have been described.⁴³ Briefly, touchscreens standardize task procedures, thereby minimizing experimenter interaction and variability across rats. Touchscreens are compatible with cutting-edge neuroscientific approaches, including chemogenetics, optogenetics, neurophysiology, and calcium imaging (using miniscopes). Touchscreens also create flexibility in experimental design and stimulus presentation. Critically, this flexibility can be used to create behavioral paradigms that are similar to human tests of cognition in terms of trial sequence, category stimuli, and analysis. Touchscreens have already been used to assess cognitive functions in rodents, including extinction, reversal learning, and 5-choice serial reaction time.⁴⁴ Our studies of category learning capitalize on the advantages of touchscreen tasks to maximize translational value.

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Here, we review our application of touchscreen-based operant procedures to investigate category learning in rodents as a tool for translational research. We focus the review on our tasks and do not attempt to comprehensively review rodent categorization. We first describe the visual capacities of rodents, as this will greatly inform the types of stimuli that can be used in category learning experiments. Second, we describe the typical task design. This includes procedures for shaping, category training, generalization testing, and a control (discrimination) task. Third, we review paradigms of category learning that are comparable in humans and rodents. Finally, we describe analysis techniques and computational modeling approaches for elucidating the cognitive mechanisms underlying category learning in rodents.

2 CAPACITIES AND LIMITATIONS OF THE RODENT VISUAL SYSTEM

Although touchscreens allow flexibility in translational research, a potential drawback to consider is that they rely on presenting visual stimuli. Indeed, the visual capacity of rodents is limited compared to humans; these perceptual differences could prevent accurate comparisons of learning between species and/or prevent learning altogether. Therefore, it is critical that visual stimuli are created with the capacities of the rodent visual system in mind. In this section, we outline the capacities of rodent vision and provide several considerations for creating stimuli that are accessible to rodents.

2.1 *Visual Acuity*

Visual acuity, or sharpness, is measured by presenting grating stimuli that contain high spatial frequencies. Maximum acuity is determined when the organism cannot distinguish a grating stimulus from a solid gray stimulus. Although humans have visual acuity as high as 30 cycles per degree, the visual acuity of pigmented rat strains (i.e., Long Evans, Dark Agouti and wild strains) is much lower (1.0 cycle per degree).⁴⁵⁻⁴⁹ Non-pigmented rats (i.e., Sprague-Dawley, Wistar, and Fischer-344), as well as mice, have even poorer visual acuity (0.5 cycles per degree), whereas the Fischer-Norway rat strain is above average (1.5 cycles per degree).⁴⁵ Therefore, fine details within stimuli may not be visible to rodents. Similar to humans, single cells in rodent primary visual cortex (V1) show frequency-tuning curves, where their firing rate decreases as the spatial frequency deviates from some optimal value. For rodents, optimal frequencies average about 0.3 cycles per degree, but cells respond to spatial frequencies as high as 1.2 cycles per degree.⁵⁰⁻⁵² Generally, their tuning curves have widths less than two octaves.⁵⁰ Most cells in V1 are modulated by spatial frequency; only 11% of cells are not sensitive to changing spatial frequencies.⁵⁰

2.2 *Orientation*

Orientation-selectivity is robust in V1 of all rat and mouse strains; 77% of V1 cells were reliably orientation-selective and only 3.5% of cells had no orientation selectivity.⁵⁰⁻⁵³ The firing rate of orientation-selective cells decreases as the presented orientation deviates from some optimal orientation value. Although all orientations are represented in V1, horizontal orientations are overrepresented.⁵⁴ In fact, 35% of orientation-selective cells peak at horizontal orientations.⁵⁰ Typically, the width of a cell's orientation tuning curve is 60 degrees or sharper.⁵⁰ Interestingly, whereas orientation-selective cells in V1 of cats and monkeys have more strict organization, orientation-selective cells of rodent V1 are much more uniformly distributed and show a salt and pepper organization.⁵⁵⁻⁵⁶ However, recent evidence suggests that V1 contains some organization according to orientation.⁵⁷

2.3 Motion

The rodent visual system can detect motion reliably. In fact, half of V1 cells respond more robustly to stimuli that drift compared to stationary stimuli.⁵⁰ Motion is typically studied using random dot patterns presented on a screen.⁵⁸⁻⁶² The proportion of dots that move in a common direction, motion coherence, can be manipulated to adjust task difficulty. The minimum coherence required to discriminate moving dots, the coherence threshold, for rats and mice is about 25% when dots move between 20 degrees per second to 100 degrees per second. This threshold is about four times larger than humans using similar parameters.⁶¹⁻⁶² Coherence

thresholds increase as dot displacement per frame increases and as frame duration increases.⁶¹⁻

⁶² Cells in V1 respond optimally to motion that ranges from 10 degrees per second to 250 degrees per second. Some cells can even respond to stimuli moving as fast as 700 degrees per second, which is faster than the feline V1.⁵⁶ V1 cells also respond to flickering gratings. Optimal flicker speeds range from 0.43 Hz to 6.88 Hz, but cells can respond to speeds up to 27.5 Hz.⁵⁰ Finally, it was recently discovered that two subregions of mouse visual cortex (LM and RL, but not V1) can detect global movement from a composite of independently moving patterns.⁶³

2.4 Color

Similar to humans, rodents have two classes of photoreceptors: rods that process black and white light and cones that process color. Color processing in rodents is limited compared to humans. Rodents have two types of cones; one type contains pigment with peak sensitivity at 358 nm and is sensitive to blue light and ultraviolet light, and another type contains pigment with maximum sensitivity at 510 nm and is sensitive to green light.⁶⁴ Within the retina, only 12% of cones are blue-type; the remaining cones are green-type.⁶⁵ Interestingly, most of the cone photoreceptors are located at the bottom of the retina. Consequently, color discrimination depends on the location of the stimulus within a rodent's visual field. For example, when mice were presented colored circles at different locations on a screen they

were sensitive to changing color when stimuli were positioned in the upper portion of their visual field, but not when the stimuli were below their visual horizon.⁶⁶

2.5 *Shape and object recognition*

Despite having lower visual acuity than humans, the rodent visual system is capable of discriminating complex shapes. Recently, it was discovered that rats, like primates, show invariant object recognition, meaning that objects are recognized despite changes in their size, color, orientation, and position on the screen.⁶⁷⁻⁶⁹ Invariant object recognition suggests that objects have complex representations that are not bound by low-level features. This is adaptive since objects are consistently experienced at different viewpoints and in varying contexts; invariant object recognition allows for spontaneous generalization to these transformations. In primates, it is proposed that this mechanism is facilitated by the ventral stream of the visual system.⁷⁰ A hierarchy exists where early visual areas predominantly process low-level features (e.g., luminance), whereas later visual areas process object-relevant features that are less sensitive to transformations in position, visual angle, etc.⁷⁰ It was recently discovered that the rodent visual system has a similar organization.^{53,71-72}

A growing number of studies have used an advanced computational approach, a bubbling technique, to understand the nature and flexibility of rat's discrimination strategies.^{41,73-76} Briefly, rats are first trained to discriminate two complex visual objects. Then,

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probe trials are presented where only a part of the object is visible (defined by the placement of small bubbles randomly dispersed across the screen). The object will be recognized only if its diagnostic features overlap with these bubbles; therefore, by averaging across many trials, a behavioral template can be created that identifies which portions of the object are necessary for recognition. Using this technique, it is apparent that rats can create templates with varying levels of complexity; this complexity is generally correlated with the difficulty of the task.⁷⁴ For example, rats will generate single-feature templates when possible but can create templates using multiple features if necessary (e.g., if an object has increased complexity or if the two objects to be discriminated are perceptually similar).^{74,76} Importantly, templates are relatively fixed when transformations of the object are presented, suggesting that the rat can rescale its template to match the transformation. Nevertheless, rats can also adapt their template to generalize to novel transformations.⁷³

2.6 Recommendations and conclusions

It is imperative to develop stimuli that are within the perceptual limits of rodents to maximize learning. It is best to use stimuli that can be distinguished by low-level features such as spatial frequency, orientation, and luminance. Stimuli with more fine details should be large enough for the rodents to see; of course, this is limited by the size of the screen. Because the rodents will be close to the screen, stimuli that are too large will exceed their field of vision. Generally,

we recommend only using black and white stimuli. Although rodents can see green and blue colors, these may not be salient cues. Finally, although the rodent visual system is well suited to detect motion, we have not been successful using motion as a stimulus dimension.

Nevertheless, assessing motion categorization in rats may be worthwhile considering its prevalence in the human and non-human primate literature.⁵⁸⁻⁶⁰

3 PRE-TRAINING PROCEDURES

In this section, we describe the necessary methodologies before category training begins. First, we provide details regarding the touchscreen apparatus used for all experimental sessions.

Second, we discuss the procedures involved to prepare each rat for category training with our paradigm.

3.1 Touchscreen apparatus

All experimental sessions are conducted within custom-built chambers (36 × 41 × 36 cm). In each chamber, a wall is outfitted with an LCD flat-screen monitor (Model 1550V, NEC, Melville, NY) so that visual stimuli can be presented to the rat. Importantly, the rat is shaped to interact with the computer monitor via an infrared touchscreen (15-in, Elo Touch Systems, Fremont, CA; see Section 2.3) positioned in front of the monitor. Single 45-mg food pellets are delivered into an aluminum food tray (6.5 × 13 × 4.5 cm) on the wall opposite the touchscreen by a rotary

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pellet dispenser (Med Associates Inc., Georgia, VT, model ENV-203IR). A relay controller (Model RS-232, National Control Devices, Osceola, MO) permits communication between the computer and the pellet relay. The wall adjacent to the monitor contains a transparent window (13.5 × 10 cm) that allows observation of the rat while inside the chamber. MATLAB (MathWorks, Natick, MA) is the primary programming software for all experimental sessions. A house light positioned above the food tray is always on during experimental sessions. A camera is mounted on the roof of the chamber and faces the screen to observe and record the rats' activity (model ELP-USB100W05MT-RL36). Finally, white noise within the experimental room is utilized to minimize distraction.

3.2 Handling and cart training

Upon reaching the animal colony, each rat is allowed one week to acclimate to the new environment. Food and water are given *ad libitum*. Then, an experimenter handles each rat daily to minimize the stress of being picked up. After one week, food restriction begins, and each rat undergoes cart training. Weights are recorded daily to ensure rats do not go below 85% of their free-feeding weight. During cart training sessions, each rat is placed on a laboratory cart, and twenty 45-mg food pellets are scattered on the cart's surface.⁷⁷ This procedure is repeated daily until the rat can successfully consume all pellets within 15 minutes

(on average, this procedure takes about 7 days). Reaching this criterion ensures each rat is acclimated to the laboratory and is encouraged to forage for experimental pellets.

3.3 *Shaping procedures*

After cart training, each rat undergoes a shaping procedure within the operant chambers. This procedure involves three separate phases; in all phases, each session includes 60 trials.

Conceptually, each phase rewards a behavior that is incrementally similar to the trial sequence used during category training (see Section 4.1). In Phase 1, each trial begins with the presentation of a star stimulus in the center of the screen. This stimulus remains on the screen for 15 seconds (or until the rat touches the screen), and then is replaced by a white box appearing on either the left or right side of the screen. If the rat touches anywhere on the screen while the white box is presented, a food reward is delivered. Otherwise, the trial times out after 45 seconds, and the trial is considered a miss. Sessions continue until the rat completes at least 55 trials within 25 minutes. In Phase 2, the rat must touch both the star stimulus and the white box to receive a food reward; otherwise, the trial is considered a miss. As in Phase 1, the star stimulus times out after 15 seconds, and the white box times out after 45 seconds. Sessions continue until the rat completes at least 55 trials within 30 minutes. In Phase 3, a black box is presented in the center of the screen after the presentation of the star and before the presentation of the white box. Here, the black box serves as a placeholder for

category exemplars (see Section 4.1). Adding the black box attempts to mimic the sequence of training trials in category learning without presenting category stimuli. In this phase, the rat must touch the star once, the black box three times, and the white box once to receive a food reward. Three touches of the black box mimics three observing touches of the category exemplar during training sessions (see Section 4.1). A pilot experiment concluded that three touches was optimal to facilitate category learning. Unlike Phases 1 and 2, the trials do not timeout. Sessions continue until all 60 trials are completed within 25 minutes. Rats typically complete all shaping procedures in about 14 days.

There is a fourth shaping phase if an alternative trial sequence is used during training (see Section 4.2). In this training trial sequence, each trial has a fixed duration, and all required touches must be completed within the time-limit to proceed. In the fourth shaping phase, the black box and the white box are presented on the screen each for two seconds. The rat must touch the black box three times and the white box once within these time windows. If successful, the rat receives a food reward. If unsuccessful, the trial aborts and repeats after a 5-10 second timeout. Sessions continue until the rat successfully completes all sixty trials within 25 minutes.

4 EXPERIMENTAL DESIGN

In this section, we outline the experimental design used to examine categorization. We first describe the typical trial sequence. Briefly, rodents initiate each trial by touching the start stimulus used in shaping, at which point a category exemplar is presented on the screen. After three observing touches of this cue, the rat must choose a left or right response key depending on the cue's category membership. A correct response delivers a food reward, and an incorrect response initiates a correction trial. Next, we describe how this trial sequence can be altered according to the demands of the task. Then, we outline general procedures for category training, generalization, and a simple discrimination task. The simple discrimination task serves as a control task to ensure that any changes in behavior across groups are specific to categorization.

4.1 *Typical trial sequence*

The typical trial sequence contains four phases, a Star phase, Cue phase, Choice phase, and Reward phase (Figure 1a).³⁷⁻³⁸ Importantly, this trial sequence separates categorization (Cue phase) from decision execution (Choice phase) and feedback processing (Reward phase), a feature that is favorable for neuroscientific approaches like optogenetics and neurophysiological recording. The trial sequence is self-paced, which ensures the rat is attending to the screen and has adequate time to 1) observe the category stimulus and 2) make

a category decision. This trial sequence has been tested only with rats; however, all procedures are applicable to mice.

On each trial, a star stimulus is presented at the center of the touchscreen (Star Phase; Figure 1a). The trial begins with one touch of the star stimulus. Next, a category exemplar replaces the star stimulus (Cue phase). This exemplar remains on the screen until the rat touches the exemplar three times. After the third touch of the exemplar, the cue disappears, and copies of this exemplar appear on the left and right side of the screen serving as response keys (Choice phase). The rat must touch either response key, according to the category membership of the stimulus. Categories are represented spatially, such that members of category 'A' should elicit a touch to the left response key, and members of category 'B' should elicit a touch to the right response key. If the rat chooses the correct side, a white box replaces the chosen response key (Reward phase). One touch of the white box delivers a food pellet. This white box acts as a secondary reinforcer and bridges the gap between the rat's decision and obtaining reward. If the rat chooses the incorrect side, a correction trial is initiated. Here, the trial is aborted and repeats from the Cue phase after a 5-10 second timeout. Correction trials repeat until the rat chooses the correct side or to a predetermined limit (e.g., two corrections) to avoid group differences in the overall number of trials. Correction trials are excluded from data analysis (see Section 6). Inter-trial intervals range from 5 to 10 seconds.

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For a direct comparison, Figure 1b outlines the trial sequence for a task examining category learning in humans. Briefly, the participant initiates each trial by pressing the spacebar (synonymous to the Star phase). Then, a category exemplar appears on the screen (Cue phase), and the participant decides its category membership by pressing either 'q' or 'p' on the computer's keyboard (Choice phase). Visual feedback is given after each category decision (Reward phase). Inter-trial intervals range from 0.8 to 1.2 seconds.

4.2 *Alternative trial sequences*

The trial sequence can be adapted in multiple ways according to the demands of the experiment. First, the touch requirement during the Cue phase can vary. Three touches of the cue was chosen to ensure the rat actively attends to the category stimulus. One strategy to enhance learning is to increase this touch requirement incrementally across sessions. However, this requirement should not exceed ten touches because this may demotivate the rat. A disadvantage of this procedure is that it increases session duration and limits the number of training trials per session. Second, the categories can be mapped to arbitrary objects instead of spatial location. For instance, the rat could touch a black box for members of category 'A' and a white circle for members of category 'B'. An advantage of this alteration is that the location of the response keys can be randomized across trials which would remove any confounds associated with a side bias. On the other hand, it is well established that rodents can easily

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form associations according to spatial location. Third, the response keys can be changed to arbitrary objects (i.e., two black boxes) with responses mapped only to spatial locations. Interestingly, category learning is facilitated when the category exemplar itself serves as a response key. This procedure minimizes working memory load and maximizes stimulus-response associations. Fourth, instead of correction trials, categories can be trained by selectively delaying reward for incorrect responses. Here, reinforcement is given after every trial, but reward delivery is delayed 1 second for trials with incorrect responses; this delay increases by 2 seconds every training session until 60 seconds is reached.³⁵ Fifth, ITIs can be increased to facilitate learning.⁷⁸ Of course, increasing ITIs also lengthens the duration of each training session.

The current trial sequence is self-paced; for some applications, this procedure may be disadvantageous. For these cases, an alternative trial sequence can be used where trial phases have fixed durations. Specifically, the Cue phase and the Choice phase are available for two seconds each, and the rat must make all touch requirements within these time windows. If successful, the trial proceeds. If unsuccessful, the trial aborts and restarts after a timeout. Two seconds was chosen based on reaction time data from prior experiments. Two seconds provides enough time for the rat to respond but does not disrupt the flow of the trial sequence. These time limits can be adjusted as necessary.

4.3 *Category training*

Typically, each training session contains approximately 80 training trials; one training session is administered daily. This maximizes the number of trials per session while ensuring the rat can complete all trials without losing motivation. However, the rat can potentially complete hundreds of trials per session and/or multiple sessions per day. Training sessions are given until a learning criterion or a set number of training sessions has been reached. Training to a criterion ensures all rats are at the same level of accuracy at the end of training. Our learning criterion is usually 75% accuracy in both categories for two consecutive sessions. It is important that both categories meet this accuracy threshold, otherwise high accuracies can be attributed to a side bias (e.g., if the rat only responds to the left response key, accuracy would be 100% for category 'A' and 0% for category 'B'). Conversely, training to a set number of sessions ensures that all rats receive an equal number of training trials. This is better suited for statistical analysis and computational modelling (see Section 6).

4.4 *Category generalization*

A hallmark of categorization is that the knowledge obtained during training can be generalized to novel exemplars.⁷⁹⁻⁸⁰ Generalization ensures that the learner has not simply memorized single exemplars but instead has learned something about the class of objects. A common test of category generalization involves presenting novel exemplars that have varying degrees of

similarity to the training set. This can be done by morphing exemplars or creating stimuli that have a mixture of features from both categories.^{67-69,71,73-76,81-83} Importantly, generalization curves can be created to observe how accuracy changes as stimuli deviate from the trained exemplars. Tests of category generalization can also examine which stimulus features control behavior. In these procedures, single stimulus features are removed, blurred, relocated, or covered.^{37,41,73-76,84-86} Generalization to these stimuli can inform how the categories were learned. For all tests of generalization, testing stimuli are intermixed among training trials. Testing stimuli are given non-differential feedback, where food reward is delivered regardless of the rats' choice and its accuracy. This prevents further learning.

4.5 Control task: Simple Discrimination

In experiments examining neural function, any change in performance across groups can be attributed to multiple constructs not specific to categorization, including movement, motivation, perception, working memory, etc.⁸⁹⁻⁹⁰ Therefore, it is essential to train rats on a control task to rule out these possibilities. For this purpose, we have used a simple discrimination task.³⁷ Here, the trial sequence is identical to category training (see Section 4.1). However, during the Cue phase, only two stimuli are presented (instead of categories of stimuli). One stimulus should elicit a touch to the left response key, and the other stimulus should elicit a touch to the right response key. Designing these stimuli deserves careful

consideration. They should have equal complexity as the category stimuli; however, they should not resemble the category exemplars because this may cause interference or generalization.

Controlling for changes in motor behavior can also be obtained by cameras that track head and eye movements.⁸⁷⁻⁸⁸

5 CATEGORY LEARNING PARADIGMS

Here, we review multiple categorization paradigms that utilize touchscreens. These paradigms span both perceptual and abstract category learning. Importantly, all tasks are compatible to neuroscientific approaches and are very similar to human category learning paradigms.

5.1 *Rule-based and information integration categorization*

Humans can develop and utilize category rules to solve category tasks.^{24,89} Typically, these rules are verbalizable and are created using a small subset of stimulus features. Rule-based (RB) learning involves testing hypotheses about potential rules and is associated with stepwise learning curves, where the steep inflection point indicates when the correct rule was selected.

To examine RB category learning, a large literature has trained participants to categorize Gabor patches, which contain black and white gratings that change in spatial frequency and orientation.⁹⁰⁻⁹² A two-dimensional stimulus space can be created using these continuous dimensions; categories are established by placing bivariate normal distributions on this two-

dimensional stimulus space (Figure 2a). Here, each point represents an exemplar with a corresponding spatial frequency and orientation, and each distribution constitutes a category. In RB tasks, distributions are perpendicular to a stimulus axis; therefore, one stimulus dimension is category-relevant and can be used to generate a unidimensional category rule (Figure 2a). Information integration (II) tasks have distributions that are 45-degree rotations of the RB distributions (Figure 2b). Here, the categories are not separable according to a single stimulus dimension, and category decisions require information from both stimulus dimensions. Therefore, for II tasks, applying a category rule leads to low levels of accuracy.

Humans and non-human primates learn RB tasks faster than II tasks.⁹³ We replicated this effect in humans (Figures 2d and e). RB tasks are learned faster than II tasks because participants approach category learning by initially searching for unidimensional category rules, a strategy that benefits RB, but not II tasks. In fact, biasing unidimensional strategies hinders learning II tasks because participants commonly apply a suboptimal strategy. Conversely, rats robustly learn RB and II tasks at the same rate (Figure 2c).^{38,40} We argue that rats do not bias unidimensional category rules; therefore, RB tasks are not privileged, and II tasks are not disadvantaged (see Section 6.3.2).³⁸ Instead, rats allocate attention according to the demands of the task (see Section 6.3.3).³⁸ Specifically, RB tasks are learned by incrementally shifting attention towards the relevant dimension, whereas II tasks are learned by dividing attention between both dimensions.

5.1.1 Generalization

Generalization can be assessed in multiple ways; all procedures involve sampling from novel parts of the stimulus space. First, we can sample novel exemplars that deviate from the training distributions along the relevant dimension (or for II tasks, the diagonal axis that separates the categories; Figure 3a).³⁸ With this manipulation, generalization curves can be created to observe accuracy as a function of distance from the category boundary. Relative to the training distributions, generalization improves for exemplars farther from the category boundary, and generalization declines for exemplars closer to the category boundary (Figure 3b).³⁸ This is also true for humans (Figure 3b). Second, we can sample novel exemplars that deviate from the training distributions along the irrelevant dimension (or diagonal axis for II tasks). Interestingly, humans generalize to these novel exemplars for RB tasks, but not II tasks.⁹⁴ The interpretation is that for RB tasks, category generalization is not affected by novel irrelevant values because attention had been shifted away from that stimulus dimension. This type of generalization has gained traction in the comparative cognition literature; unfortunately, the animal results are unclear. For instance, macaques also generalize robustly to novel irrelevant values in the RB task, supporting the claim that macaques can apply category rules like humans.⁹⁵ However, this effect was not replicated.⁹⁶

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There is a second motivation for examining generalization along the irrelevant dimension in RB tasks. In humans, it is well known that spatial frequency and orientation are perceptually separable stimulus dimensions, meaning that both dimensions can be processed independently from the other.⁹⁷⁻⁹⁸ Conversely, for perceptually integral dimensions, the value of one dimension influences the perception of another dimension.⁹⁷ This issue becomes relevant for learning RB tasks, where rule use depends on differentiating a category-relevant dimension and a category-irrelevant dimension. Indeed, rule use is more difficult if the dimensions are perceptually integral.⁹⁹ Although formal tests exist to assess perceptual separability,⁹⁷ an alternative approach is to examine generalization along the irrelevant dimension for values that fall outside of the range of trained stimuli. For separable dimensions, generalization should be independent of the value of the irrelevant feature. For integral stimulus dimensions, generalization along the irrelevant dimension in the RB task would decline rapidly. On the other hand, other factors may complicate how the results are interpreted (e.g., novel stimulus values along irrelevant dimensions may attract attention simply because they are unfamiliar).

5.1.2 Task switching

In addition to generalization tests, rule switches can be implemented after category learning. For example, training distributions can be rotated 90 degrees (Figure 4a). With this

manipulation, the irrelevant dimension becomes relevant and vice versa for RB tasks. This is synonymous to an extradimensional shift, where attention is shifted to a new perceptual dimension.¹⁰¹ For II tasks, the relevant *axis* becomes irrelevant and vice versa. This is synonymous to an intradimensional shift, where the same dimensions are relevant, but values along each perceptual dimension are remapped to different behavioral responses.¹⁰¹ Notably, with this 90-degree rotation, category membership changes for only 50% of the category stimuli (Figure 4a; right). This may provide an additional advantage; it is possible to observe within-session how rodents approach stimuli with a new category response vs. stimuli with the same response (Figure 4b).

5.2 Statistical Density

From the human literature, it is known that the ratio between category-relevant and category-irrelevant features affects category learning.¹⁰¹ Generally, spatial attention should be directed towards the category-relevant features and away from the irrelevant features. Therefore, attention becomes more selective and constrained when categories contain fewer category-relevant features. In this paradigm, the ratio of category-relevant and category-irrelevant features can be manipulated easily.¹⁰² For humans, categories with many category-relevant features (i.e., Dense) can be learned at a young age and with minimal feedback, whereas categories with few category-relevant features (i.e., Sparse) require consistent feedback to find

the few relevant features.¹⁰² In the rodent version of the task, stimuli are structured in a pentagon configuration, and single features are placed at each corner of the shape (Figure 5a).³⁷ For Dense categories, features in three locations provide deterministic category membership (i.e., category-relevant features), and the features in the remaining two locations provide no information regarding category membership (i.e., category-irrelevant features). For Sparse categories, only the features in one location determine category membership, and the rest are irrelevant. The location of category-relevant and category-irrelevant features are fixed for both Dense and Sparse categories. Luminance is controlled across all features so that brightness cues cannot be used to solve the task. Rats consistently learn Dense categories faster than Sparse categories and require consistent feedback to learn both task types (Figure 5b).^{37,42}

This stimulus set offers multiple tests of category generalization.³⁷ First, novel category exemplars are stimuli that retain the category-relevant features but have new category-irrelevant features (Figure 5c). Rats generalize to novel exemplars, suggesting that attention had been shifted towards the category-relevant features and away from the category-irrelevant features (Figure 5d).³⁷ Second, in relocated exemplars, category-relevant features are shuffled to locations that normally contained category-irrelevant features. Generalization to these stimuli is reduced for rats, especially for Sparse categories, suggesting that rats learn about both the identity and location of category-relevant features. Third, singleton exemplars consist

of a single category-relevant feature. Generalization is reduced for these stimuli as well, suggesting that rats encode the entire stimulus structure and do not simply search for category-relevant features within the stimuli.

5.3 *Naturalistic Categories*

Although artificial stimuli have great flexibility in controlling category-relevant and category-irrelevant features, it is important to assess whether rats can also learn naturalistic categories. For instance, we have successfully trained rats to categorize images of chairs, flowers, people and cars (Figure 6a).³⁵ Rats have also been trained to categorize human faces, man-made artifacts, animals, and movies containing rats.^{39,41,75} Generalization can be tested by presenting novel exemplars, relocating images, rotating images, or covering portions of the training stimuli to determine which features and dimensions influence the subject's behavior.^{35,39,41} Generally, creating these stimulus sets is challenging because it is necessary to control for low-level features such as brightness, spatial frequency, and size in naturalistic stimuli. Furthermore, images should be chosen that contain few fine details because of the limited visual acuity of rodents.

5.4 *Abstract Categories*

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For abstract categories, learning is based on dimensions that are not inherent to the stimuli themselves. For example, rats can learn to discriminate ‘same’ vs. ‘different’ stimulus arrays.³⁶ In this design, an array of objects is presented on each trial. For members of the category ‘same,’ all the objects within the array are identical; for members of the category ‘different,’ the objects are all unique (Figure 6b). A unique set of objects is used for each trial. Multiple species, including humans, baboons, and pigeons, discriminate these categories by comparing each array’s entropy, which is a measure of variability or diversity.¹⁰³ Whereas exemplars of the category ‘same’ contain 0 entropy, exemplars of the category ‘different’ contain positive entropy. Understanding the neural underpinnings of abstract categorization in rodents may be extremely informative, as abstract categorization is prevalent in human category learning and is foundational for understanding abstract ideas like justice and peace.¹⁰⁴

6 DEPENDENT MEASURES AND ANALYSIS

In this section, we review common analyses used with our multi-phase paradigm. We first outline the quantitative dependent measures that are used to assess learning and generalization. Then, we demonstrate how advanced techniques like machine learning and computational model fitting can be used to elucidate the cognitive mechanisms of category learning. Critically, because the task design is compatible for both rodents and humans, analyses can be directly compared across species.

6.1 *Dependent measures*

Four main dependent measures are applicable to the current paradigm: accuracy, response time, touch separation, and response bias. Accuracy is defined as the proportion of correct responses during the Choice phase, excluding correction trials. Response time can be measured for each trial phase and can calculate the duration to categorize the stimulus (Cue phase) and execute a category decision (Choice phase). Touch separation uses the pixel location of touches during the Cue phase as a measure of choice anticipation.³⁷ As the rat learns the categorization task, the three touches during the Cue phase deviate horizontally towards the correct side (left for members of category A and right for members of category B). Touch separation is calculated by subtracting the x-coordinate of the touch from the average x-coordinates of all touches during the Cue phase and averaging across all correct trials. A positive touch separation corresponds to x-deviation towards the correct side, and negative touch separation corresponds to x-deviation towards the incorrect side. Consistently, touch separation increases across learning and is highly correlated with session accuracy (Figure 7). Also, touch separation can be calculated for each of the three touches during the Cue phase. Generally, touch separation is larger for the third touch compared to the first touch (Figure 7). Touch separation can also be calculated using the y-coordinate of each touch; however, separation along the vertical dimension is not robust. Combining touch separation with reaction time can model the

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decision-making process across learning (i.e., Drift-diffusion models).¹⁰⁵⁻¹⁰⁶ Response bias measures the relative number of responses to the left response key and the right response key to gauge side bias. Response bias is calculated using the following equation:

$$\text{Response bias} = \frac{|Left - Right|}{Left + Right},$$

where Left is the number of trials the rat chose the left response key, and Right is the number of trials the rat chose the right response key. This measure ranges from 0 to 1, where 0 means no side bias and 1 means complete side bias. These dependent measures can thoroughly describe category learning and generalization across and within sessions.

6.2 Machine learning

Machine learning is an application of artificial intelligence that learns through experience without being explicitly programmed.¹⁰⁷⁻¹⁰⁸ Typically, a machine learning classifier is trained with a dataset and the performance of the classifier is assessed according to how well it can generalize to novel exemplars. Machine learning can be applied to the current design by comparing the classifier's performance across training or experimental conditions. The classifier can be trained with any dependent measure; here we discuss touch separation. As described, touch separation relates to choice anticipation. As the rat learns the category task, the pixel location of the three touches during the Cue phase deviates towards the correct side. To verify that these touch patterns convey information regarding category membership, a support vector

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machine classifier was trained with 1) the x-coordinates of the three touches during the Cue phase and 2) the trial's category membership.^{37,109} Leave-one-out cross validation was used to test the classifier, such that the classifier was trained with all but one trial and tested with the remaining trial.¹¹⁰ This process was repeated for all trials. Importantly, the classifier had higher performance for sessions later in category training compared to earlier sessions (Figure 8a). This supports the results that touch separation is correlated with accuracy and indicates that this measure of choice anticipation develops as the rat learns the task. In a second analysis, the classifier performed better when it was trained with information from the third touch vs. the first touch (Figure 8b), supporting the idea that touch separation is related to the decision-making process.

6.3 Model fitting

Fitting computational models to behavioral data can inform the learning process by providing estimates of measures that are not obtainable by accuracy alone, including how attention is distributed across stimulus features and how categories are represented by the learner. These measures can be compared across training and/or experimental conditions to elucidate mechanisms of category learning.

6.3.1 Generalized Context Model

The GCM (Generalized Context Model) is a computational model that can assess how attention is distributed across stimulus dimensions.¹ GCM is inspired by exemplar theory, which is a long-standing theory of categorization that assumes categories are represented by multiple instances of the category previously experienced by the learner. In GCM, each instance is stored in memory as a point in an n -dimensional space, where n is the number of perceptual dimensions within the category stimuli (e.g., spatial frequency and orientation of Gabor patches). Making a category decision involves calculating the perceptual similarity between the current exemplar and all exemplars stored in memory. Specifically, the probability of assigning some exemplar i to some category a is the ratio between the similarity of the exemplar to all members of category A and the similarity of the exemplar to all members of all possible categories (see Supplemental Materials for more information).

GCM has an attentional mechanism that can stretch or shrink each stimulus dimension according to importance. This type of attention affects how perceptual similarity is calculated and allows stimulus information from category-relevant dimensions to contribute more to the category decision. Mathematically, this is accomplished by adding free parameters, w , that weight each stimulus dimension. A large attention weight stretches a stimulus dimension and exaggerates distances along that dimension. A small attention weight shrinks a stimulus dimension and therefore distances along that dimension are ignored. These weights transform the stimulus space to reflect selective attention.

We recently applied GCM to estimate how rats distributed attention in RB and II categorization tasks (Figure 9a).³⁸ Here, we presented the model with exemplars used during generalization sessions. We then optimized GCM's performance to these exemplars such that the model's predictions matched each rats' behavior. This was accomplished by optimizing GCM's free parameters (including the attention weight parameter; see Supplemental Materials for more information). For rats that learned an RB task, the estimated attention weight for the category-relevant dimension was high, and the estimated attention weight for the category-irrelevant dimension was low (Figure 9b). Therefore, GCM predicted that rats learned the RB tasks by devoting more attention to the category-relevant dimension and ignoring the irrelevant dimension. For rats that learned an II task, estimated attention weights were equivalent for both stimulus dimensions (~ 0.5). Therefore, GCM predicts that rats learned the II tasks by dividing attention between the two dimensions. Together, these results suggest that rats distributed attention according to the demands of the task; selective attention was used to learn the RB tasks, and divided attention was used to learn the II tasks. This information provides insight into the capabilities of rodent category learning and informs neurobiological experiments that examine the neural basis of selective attention.

6.3.2 Decision Boundary Analysis

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GRT (General Recognition Theory) is a second computation model of categorization that can inform the type of strategy used by the learner to make a category decision.¹¹¹ Specifically, GRT assumes that the learner places a decision boundary onto the stimulus space (see Supplemental Materials for more information). This boundary segregates the space into distinct regions; each region is assigned a unique category label. For instance, category 'A' is assigned for stimuli that fall on one side of the boundary, and category 'B' is assigned for stimuli that fall on the other side of the boundary. Linear boundaries are common; however, decision boundaries can take many forms (e.g., quadratic). Linear boundaries can be created using either a single stimulus dimension (synonymous to an RB strategy) or multiple stimulus dimensions (synonymous to an II strategy). A RB linear decision boundary is a line that is perpendicular to the category-relevant dimension. An II linear decision boundary, on the other hand, is a line that can have any slope. Generally, multiple models are fit to each rats' data, where each model creates a decision boundary using a different strategy (e.g., RB or II strategies). The best fitting model is assumed to be the strategy used by the learner.

We recently applied GRT to estimate the strategy used by rats that learned RB and II categorization tasks.³⁸ For this analysis, three models were fit to each rats' generalization data separately. Two models used RB strategies and created linear decision boundaries using a single stimulus dimension (i.e., spatial frequency or orientation). A third model used an II strategy and created linear decision boundaries using both stimulus dimensions (i.e., spatial frequency and

orientation). The model that best fit the rat's behavior was assumed to be the strategy utilized by the rat (i.e., either an RB strategy or an II strategy; see Supplemental Materials for more information).¹¹² We found that all rats that learned an II task were best fit with the model using an II strategy. Thus, rats learning the II tasks successfully applied the correct strategy. Figure 9d shows the best fitting decision boundaries for rats that learned an II task. Each point designates a testing stimulus presented during generalization sessions, and each line is the best-fitting decision boundary for a single rat. Notice that all lines are sloped. For rats that learned an RB task, only half of the rats were best fit with a model that used an RB strategy (10/24).³⁸ Figure 9c shows the best fitting decision boundaries for these rats; notice that about half the boundaries are perpendicular to an axis (i.e., an RB strategy) and the other half have a slight slope (i.e., an II strategy). These results indicated that some rats learning the RB tasks were using both stimulus dimensions to make their category decisions and therefore were still somewhat controlled by the category-irrelevant dimension. These results combined with the GCM fits suggest that rats learning RB task can shift attention towards the relevant dimension, but do not reliably divert all attention to this dimension as humans do. Incomplete selective attention may result from an inability to inhibit irrelevant information or may reflect a strategy that attempts to avoid costs associated with selective attention.¹¹³

6.3.3 SUSTAIN

SUSTAIN (Supervised and Unsupervised STRatified Adaptive Incremental Network) is a neural network model of category.¹¹⁴ SUSTAIN is considered a clustering model, which means that it stores related exemplars together in memory. Similar to GCM, SUSTAIN contains an attention mechanism that estimates how each stimulus is weighted. Unlike GCM, SUSTAIN can track changes in attention across training trials. Here, we trained SUSTAIN to learn RB and II categorization tasks and then fit SUSTAIN's performance to both rat and human learning data (see Supplemental Materials; Figures 10a-b). As described below, this allowed us to estimate abstract measures like selective attention and category representation.

Similar to GCM, SUSTAIN contains a mechanism that prioritizes distances along category-relevant stimulus dimensions (i.e., selective attention). At the beginning of training, each dimension is assigned an equal attention weight (i.e., diffused attention). After every trial, these attention weights can shift towards category-relevant dimensions. The rate of change of the attention weights is determined by a free parameter (i.e., attention learning rate). We found that to learn RB tasks, SUSTAIN shifted attention towards the category-relevant dimension and away from the category-irrelevant dimension (Figure c). This was true when SUSTAIN was fit to both rat and human learning data. Notice SUSTAIN predicts that attention to the relevant dimension increases over training trials, whereas attention to the irrelevant dimension decreases over training trials. This pattern is similar between rats and humans, but the time scale is much faster for humans. To learn II category tasks, SUSTAIN predicts that

attention is split between both dimensions across training. This was true for both rats and humans. Together, these results agree with GCM and support that rats learn RB tasks by shifting attention to the relevant dimension. SUSTAIN expands on these results by detailing how attention shifts across training.

Under SUSTAIN, categories are represented by one or multiple clusters. Each cluster reflects prior training experience(s) and is positioned in an n -dimensional space, where n is the number of perceptual dimensions contained within the training stimuli (i.e., spatial frequency and orientation). On each trial, clusters are activated according to the distance between the cluster and the current exemplar, where cluster activation decreases with increasing distance. Then, the cluster with the highest activation is the winner and initiates a probabilistic category decision. At the beginning of training, SUSTAIN contains a single cluster centered at the position of the first training exemplar. If the model makes a correct response, that trial's exemplar is integrated into existing category representations, such that the position of the winning cluster is shifted in the direction of that exemplar. If an incorrect response is made, the complexity of the category representation increases, such that a new cluster is recruited and is positioned on the misclassified exemplar. Importantly, the number of clusters at the end of training can inform how categories were learned and represented. We found that to learn RB category tasks, SUSTAIN recruited two clusters (one for each category). This was true when we fit SUSTAIN to both rat and human learning data and suggests that RB categories were

represented by single prototypes (Figure 10d). Conversely, SUSTAIN recruited multiple clusters (4-5 per category) to learn II tasks. This was true for both rat and human data and suggests that II categories were represented through multiple exemplars (Figure 10d). The similarity in how rats and humans represent these category tasks hints at common neural mechanisms underlying category learning between species. It also suggests that the category structure itself has a large impact on how categories are learned.

7 CONCLUSIONS

We have capitalized on the advantages of touchscreen-based operant tasks to study the cognitive and neural mechanisms of category learning in rats. The flexibility of visual stimulus presentation has made it possible to examine several different types of categories and to quantitatively assess key factors in categorization such as statistical density, stimulus dimensions, and generalization functions. We have also demonstrated that the quantitative dependent measures from these categorization tasks are ideal for computational modeling of category learning. These category learning tasks are also well suited for various neuroscience methods such as neurophysiology, in vivo imaging, and optogenetics. Lastly, the touchscreen tasks are very similar to tasks used in humans, indicating extraordinary potential for translational research on categorization.

We have used touchscreen-based tasks to examine learning of artificial, naturalistic, and abstract categories in rats. These tasks have also enabled us to examine various aspects of category structure and top-down goal-directed attention in rats. Artificial stimuli allow for complete control in the statistical density of category-relevant vs. category-irrelevant dimensions, a common manipulation in human category learning that examines how attention is distributed according to the demands of the task. These stimuli are also well suited for additional designs, including probabilistic category structures, where each stimulus feature probabilistically predicts category membership, and polymorphous category tasks, where a stimulus is a member of a category if it contains at least m out of n category-relevant features.^{17,115} Naturalistic categories allow for greater external validity and can investigate how these experimental procedures generalize to real-world categories. Finally, abstract categories examine the ability to extract features that go beyond perceptual similarity. We discussed 'same-different' categories, but abstract category tasks can also assess concepts like symmetry, number cardinality, and number ordinality.¹¹⁶⁻¹¹⁷

A clear advantage of touchscreen-based category learning tasks lies in the flexibility of potential analyses that go beyond accuracy and reaction time. As described, these include touch separation, machine learning, and computational model fitting, which together provide estimates of more abstract measures like choice anticipation, selective attention, and category representation. These analyses are crucial for translational studies because they provide

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boundaries for the interpretation of experimental findings. For example, the fact that rats can learn RB tasks does not indicate that they use rules to solve the tasks like humans.³⁸ Likewise, the fact that they do not show faster learning of RB tasks cannot be attributed to the absence of executive function.³⁸ Therefore, by employing advanced analyses available to this methodology, we have a deeper understanding of the nature of rodent category learning.

A second advantage of the current paradigm is that comparing categorization between rodents and humans becomes much more direct. For both rodents and humans, the trial sequence is self-paced and requires the participant to identify the category membership of the current stimulus by making one of two alternative responses. Therefore, both rodent and human participants can be trained with similar trial procedures and stimulus sets, and measures of reaction time and accuracy become relevant to compare category learning and generalization between species. These similarities also lend themselves well to computational modelling. For example, by fitting models like SUSTAIN to data from both species, we can compare selective attention and category representations. Specifically, we conclude that both rats and humans use selective attention to learn the RB tasks, but not the II tasks. Additionally, RB categories are typically represented by a single cluster (i.e., prototype), whereas II categories are represented by multiple clusters (i.e., exemplar).

These similarities between rodent and human tasks add translational value and validity for using rodents to examine neural mechanisms underlying categorization. Testing clinical

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populations directly can be difficult, and results are often affected by undesired confounds. Cutting-edge neuroscientific approaches provide high selectivity, specificity, and reliability to understand mechanisms from key brain regions that are implicated in neuroimaging studies and are affected in clinical populations, including the prefrontal cortex, hippocampus, and basal ganglia.¹¹⁸⁻¹²⁰ Manipulating neural activity using techniques like optogenetics, chemogenetics, and local pharmacology can establish the necessity and sufficiency of activity in each brain region in categorization. Recording single unit neuronal activity in multiple regions simultaneously can elucidate how regions interact within trials and across learning. Finally, genetic manipulations create models of cognitive disorders that can test hypotheses of the underlying mechanisms. Together, research with rodent models will lead to a better understanding of how the brain mediates category learning. This information may inform novel treatments and medications for multiple cognitive disorders.

Combining these neuroscientific techniques with computational approaches becomes a powerful tool for leveraging strong claims about neural function. For example, a recent theory of category learning, EpCon (Episodes-to-Concepts), posits that category learning is accomplished through a close interaction between prefrontal cortex and hippocampus.¹³ EpCon is a neural interpretation of SUSTAIN, where prefrontal cortex shifts attention towards category-relevant dimensions and hippocampus stores category representations. Using the current design, the EpCon framework can be tested directly. For example, parameter estimates

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in SUSTAIN can be compared between control groups and rodents with selective inactivation of either the prefrontal cortex or hippocampus. This combination of neuroscientific and computational approaches (and others) will yield a much deeper understanding of the mechanisms underlying category learning and how they can be impaired in ADHD, Parkinson's, schizophrenia, and amnesia.

One limitation of touchscreens is that it is difficult to control factors like viewing angle and position. A solution is to use a design where the rodent's head is semi-fixed.^{69,121} In this design, rats view a computer monitor by placing their head through a small hole in the wall of an operant chamber. This hole limits head movement; therefore, distance from the screen and viewing angle are kept constant. The rat completes trials by interacting with touch sensors and feeding needles that deliver liquid reward. With this design, it is possible for the rodent to complete hundreds of trials per session, which increases the feasibility of conducting computationally intensive analyses.⁶⁹ Second, head-fixed designs are common, especially for research using mice.¹²²⁻¹²³ By restricting head movements, it is much easier to control the presentation of visual stimuli and conduct invasive neuroscientific approaches like calcium imaging and *in vivo* neurophysiological recordings. With this design, it is common to project virtual environments onto computer screens. Then, the rodent can navigate these environments by moving a cylindrical treatmill.¹²²⁻¹²³

To conclude, our current use of touchscreen-based operant procedures offers a framework for examining the neural mechanisms of category learning. These touchscreen paradigms have flexibility in experimental design, category stimuli, and analysis strategies. Moreover, these paradigms are directly applicable to human tasks of categorization, facilitating comparisons of category learning between species. These touchscreen-based procedures are also readily used with cutting-edge neuroscientific methods such as optogenetics, chemogenetics, *in vivo* neurophysiology, and calcium imaging (using miniscopes). The combined use of these neuroscientific methods and computational modeling is a very powerful approach for elucidating the mechanisms underlying cognition and pathological conditions that impair it.

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DATA AVAILABILITY STATEMENT

The data for the rat and human tasks are openly available in Dryad at: <https://doi.org/10.5061/dryad.qv9s4mwbm>. Codes for the tasks and a list of hardware for the touchscreen apparatus are available at: <https://github.com/FreemanlabUlowa/RodentCategorization>.

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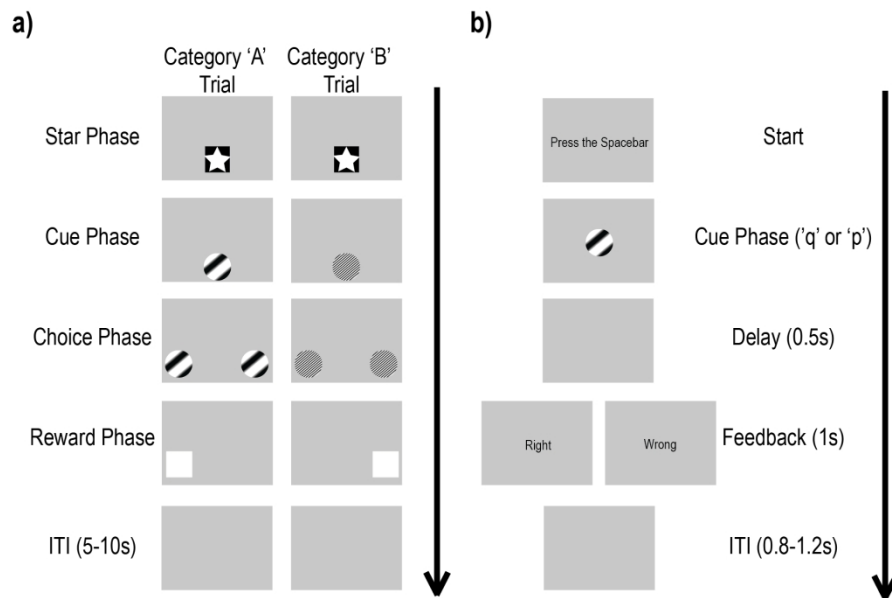


Figure 1. a) The trial sequence used for category training and testing sessions for rodents. The trial begins with the presentation of a start stimulus (Star phase). The rat initiates the trial by pressing the star stimulus once, at which point a category exemplar appears on the screen (Cue phase; a Gabor patch is shown as an example). The rat must touch the exemplar three times, at which point copies of the exemplar appear on the left and right sides of the screen, acting as report keys (Choice phase). The rat makes one touch to either side, depending on the category membership of the stimulus (i.e., touch the left exemplar for members of category 'A', and touch the right exemplar for members of category 'B'). If the rat chooses the correct side, a white box appears (Reward phase). One touch of the white box delivers a food reward. If the rat chooses the incorrect side, a correction trial is initiated such that the trial repeats from the Cue phase after a 5-10 s timeout. b) The typical trial sequence used for category training and testing sessions for human participants. After a press of the spacebar, a category exemplar appears on the screen (Cue phase). Then, the participant must press either 'q' or 'p' on the keyboard depending on the category membership of the stimulus (i.e., 'q' for members of category 'A' and 'p' for members of category 'B'). Then, visual feedback is given.

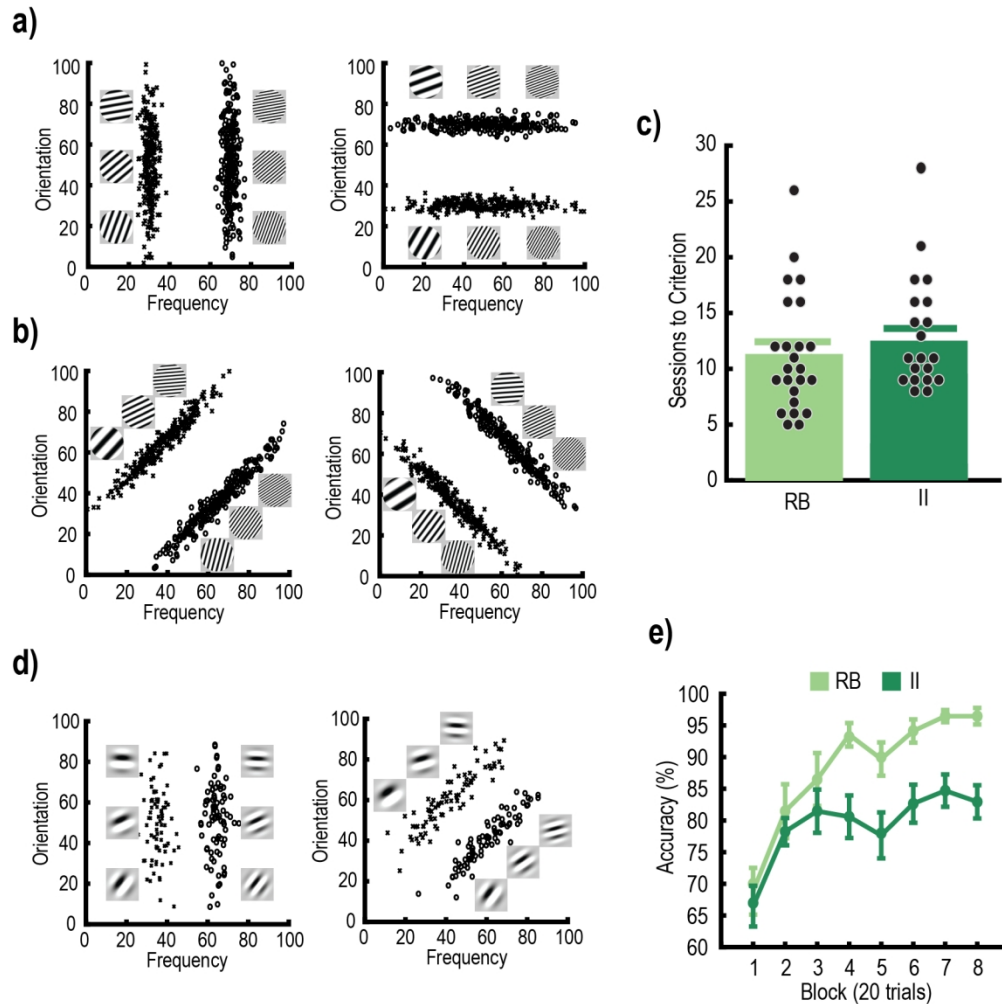


Figure 2. a) Rule-based (RB) category distributions used for rodents. Here, normal distributions are placed on a two-dimensional space (e.g., the spatial frequency and orientation of gratings). Each distribution constitutes a category and each point represents a category exemplar. RB distributions are perpendicular to an axis and are learned by attending to this dimension. b) Information integration (II) category distributions. II distributions are simply 45-degree rotations of RB distributions. Importantly, categorizing these stimuli require information from both stimulus dimensions. c) For rats, a similar number of sessions is required to reach a learning criterion (75% accuracy in both categories, 2 consecutive sessions) for both RB and II task types. d) RB (left) and II (right) category distributions used for humans, with a Gaussian filter added to the stimuli. e) Humans reach higher accuracy levels for the RB tasks compared to the II tasks. Data in c redrawn with permission from reference 38.

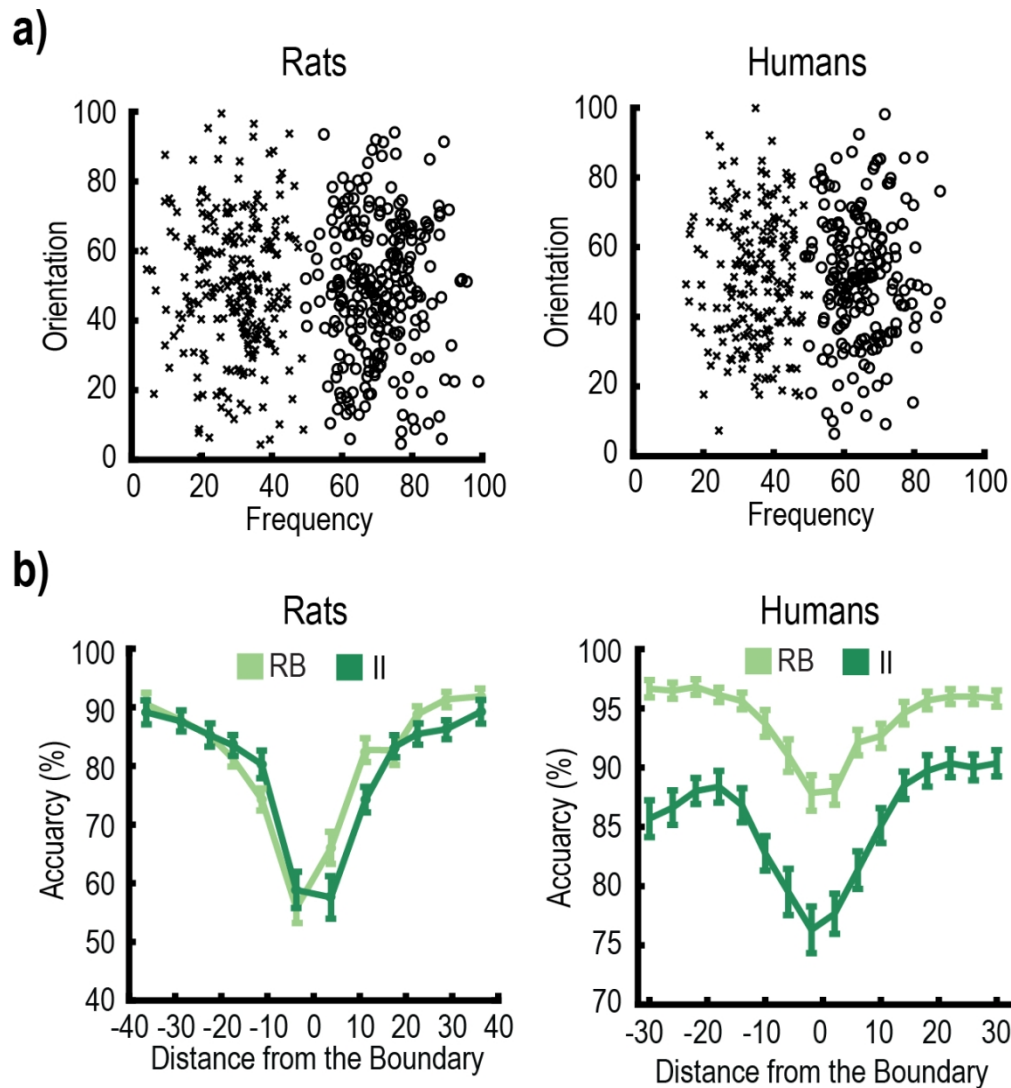


Figure 3. a) For rats (left) and humans (right), generalization was examined by creating category distributions with the same category means but larger standard deviation along the relevant dimension (or axis in II tasks). b) Accuracy was calculated according to distance from the category boundary. For both task types, the boundary is defined as a line that segregates the two categories. For RB tasks, this line is perpendicular to a stimulus axis and therefore distance from the boundary is in units of the category-relevant dimension (e.g., either spatial frequency or orientation, depending on the task). For II tasks, the line is sloped and therefore distance from the boundary is in units that combine both stimulus dimensions. Specifically, distance from the boundary refers to the Euclidean distance between the stimuli and the sloped line that segregates categories 'A' and 'B'. For rats (left) and humans (right), accuracy improves as a function of the distance from the category boundary, which is observed for both RB and II tasks. Data in a and b redrawn with permission from reference 38.

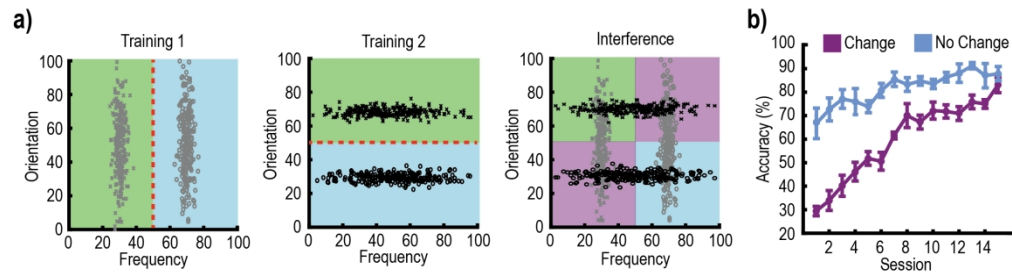


Figure 4. a) Multiple rule-reversals are possible with the current design. After category training (left), category distributions are rotated 90 degrees (middle). As a result, the relevant dimension becomes irrelevant in RB tasks, and the relevant axis becomes irrelevant in II tasks. Importantly, only half of the stimulus space changes category membership (right; portions in purple). b) Pilot experiment where rats were given 15 training sessions to learn an RB task (not plotted). Then, rats were given 15 training sessions to learn distributions that were rotated 90 degrees from their initial training. Accuracy is plotted for stimuli that changed category membership after the reversal (Change) and stimuli that did not change category membership after the reversal (No Change). Notice that accuracy for No Change stimuli are well above chance, suggesting that rats maintained this category knowledge from the previous training. Accuracy for Change stimuli is first below chance and then increases as training progresses.

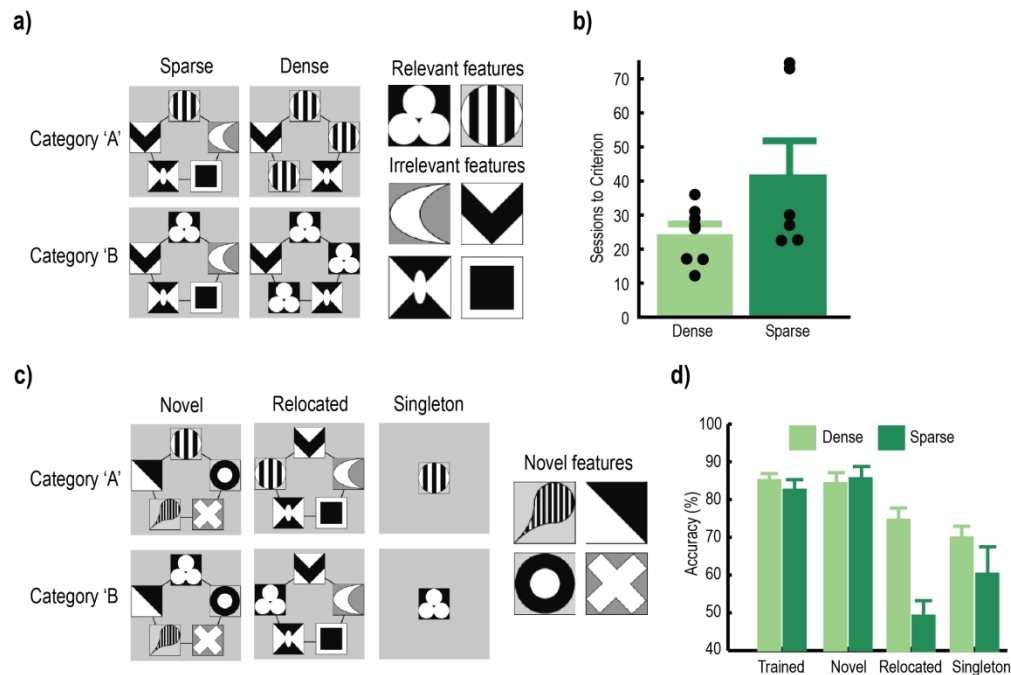


Figure 5. a) Artificial stimuli are arranged in a pentagon configuration and relevant or irrelevant features are placed at each node. In Sparse categories, the feature at the top location determines category membership and the other locations vary randomly. In Dense categories, the features at the top, upper left and lower right all determine category membership. b) Rats typically learn Dense categories faster than Sparse categories, as each stimulus contains a higher proportion of category-relevant information. c) Example testing stimuli from Sparse categories. Novel stimuli contain new irrelevant features. In Relocated stimuli, the relevant feature(s) are moved to locations typically containing irrelevant features. Singleton stimuli are simply the presentation of relevant features. d) Typical accuracy for the testing stimuli. Rats generalize to Novel stimuli but show generalization decrements to Relocated and Singleton conditions. Data redrawn with permission from reference 37.

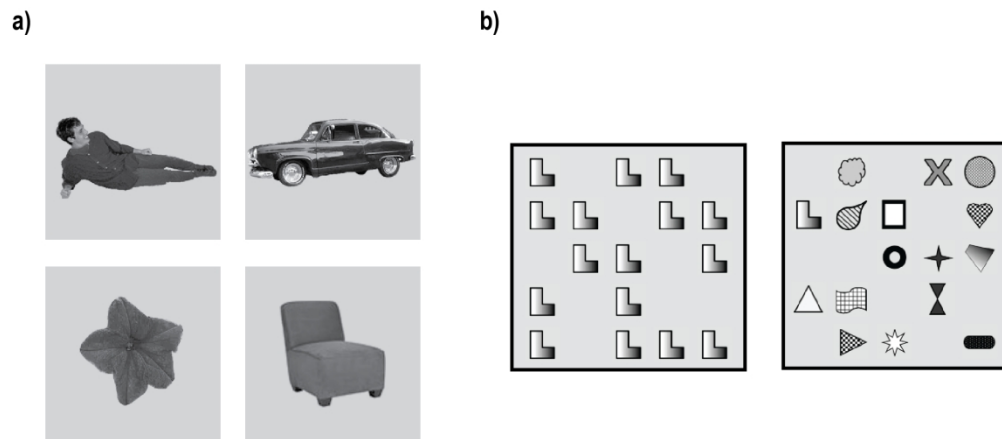


Figure 6. a) Example stimuli from naturalistic categories learned by rats. Rats discriminated images of people vs. cars and flowers vs. chairs. Images were controlled for lower level features like brightness. Then, novel images were presented to examine category generalization. b) Example stimuli from abstract categories learned by rats. Here, stimuli contained sixteen icons randomly distributed on the screen. The icons of members of the category 'same' (left) were all identical, whereas the icons of members of the category 'different' (right) were all different.

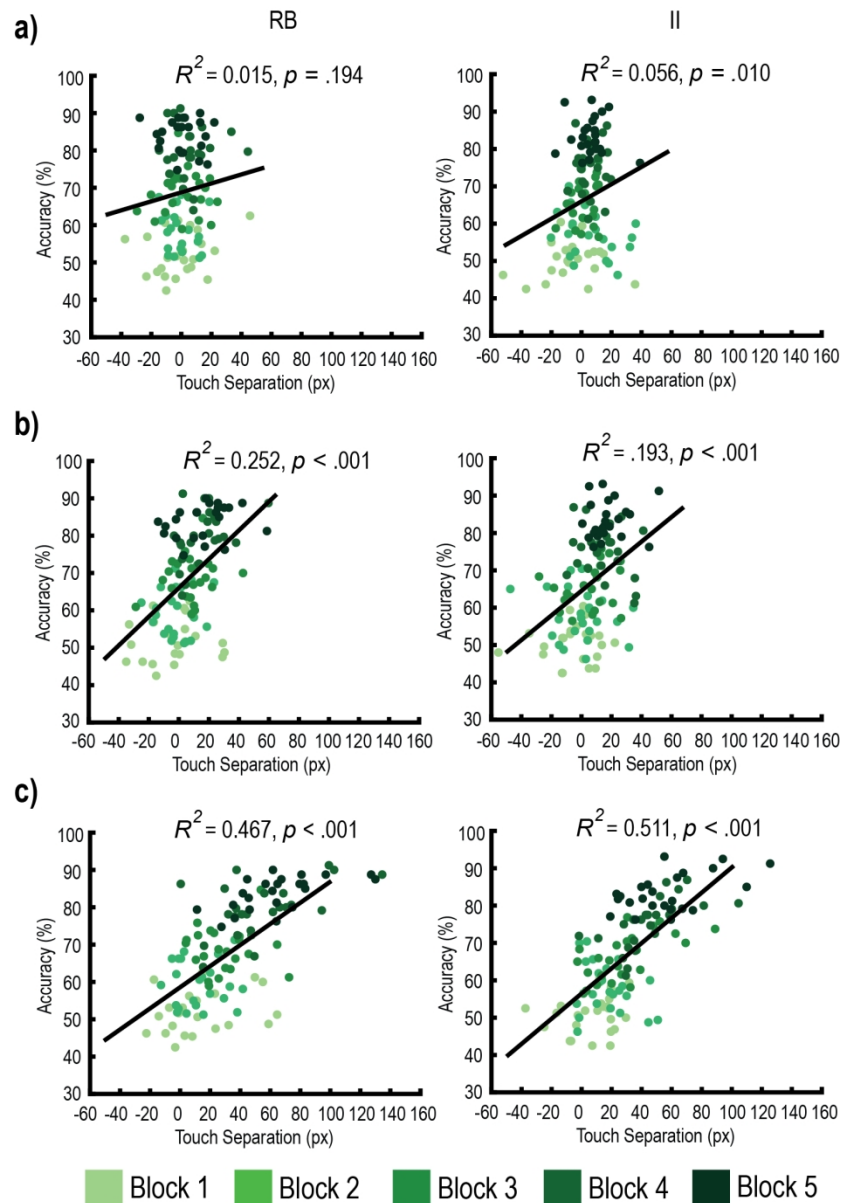


Figure 7. Touch separation is calculated using the x-coordinate of touches during the Cue phase. As accuracy improves, these touches deviate towards the correct side in anticipation of the rats' decision. Here, we present correlations between touch separation and accuracy for rats learning RB (left column) and II (right column) category learning tasks. For this experiment, rats were presented training sessions until they reached a learning criterion.³⁸ As a result, each rat was presented with a different number of training sessions. To ensure that each rat contributed an equal number of samples to the analysis, training sessions from each rat were vincintized into five training blocks (blocks 1-5). So, if the rat took 10 training sessions to reach the learning criterion, each training block represents the average of two training sessions. Touch separation was calculated according to the first touch (a), second touch (b), and third touch (c) during the Cue phase. Importantly, correlations between touch separation and accuracy are larger for the third touch compared to the first touch.

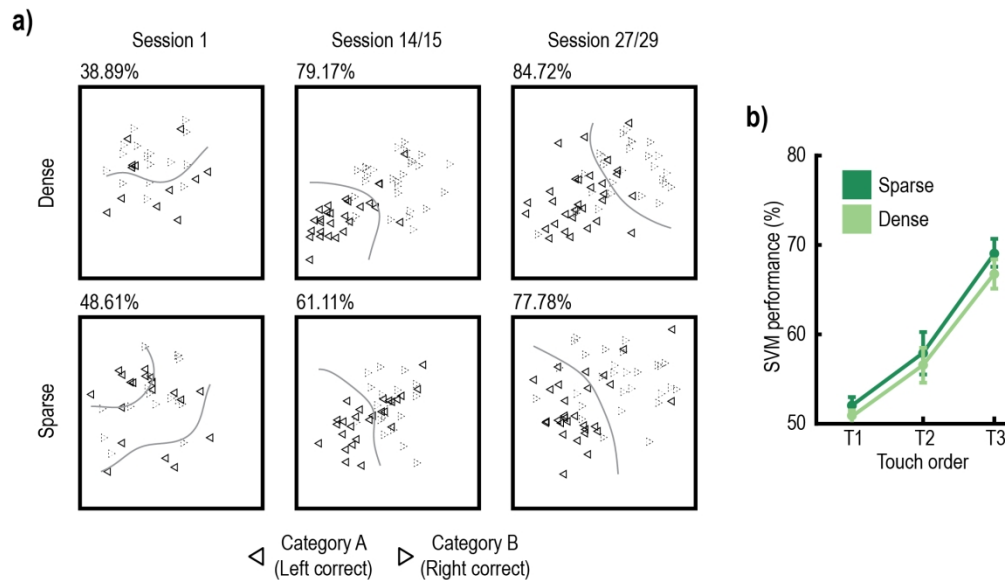


Figure 8. a) SVM was trained with touch information (i.e., the x and y coordinate) of touches during the Cue phase of correct trials.³⁷ These results come from individual rats learning either Sparse (bottom) and Dense (top) categories. SVM's accuracy in predicting category membership (indicated by the number above each box) improved when it was trained with touch information from later training sessions, suggesting that touches convey category information as the rat learns the category task. b) In a separate analysis, SVM was trained with touch information (i.e., the x and y coordinate) of touches during the Cue phase of correct trials from all training sessions. The classifier's accuracy in predicting category membership was higher when it was trained with information from the third touch compared to when it was trained with information from the first touch. Therefore, category information increases with the touch number. This pattern is true for rats learning both Dense and Sparse categories. Data redrawn with permission from reference 37.

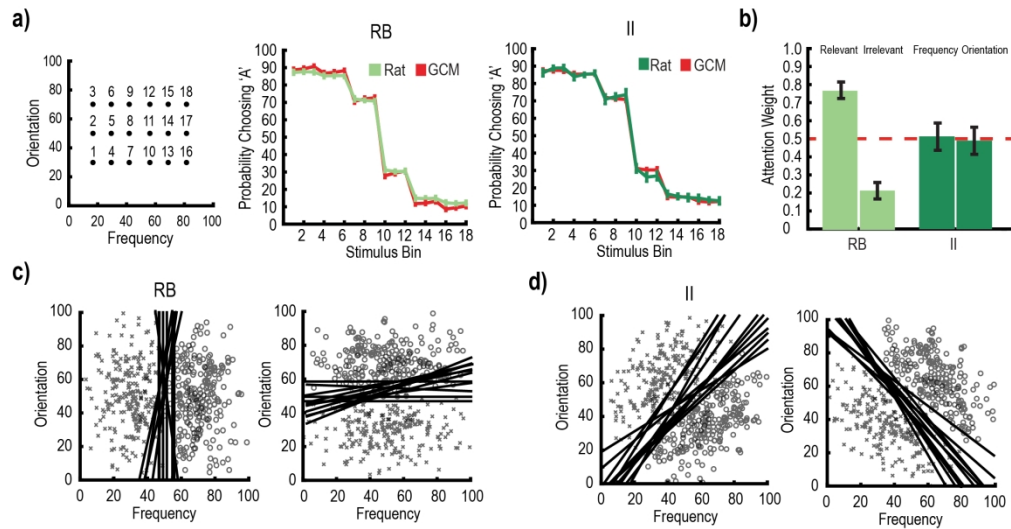


Figure 9. a) GCM was successfully fit to the generalization data of rats that had learned either an RB (left) or II (right) task.³⁸ To visualize the model's performance, stimuli within the generalization distributions were averaged into 18 distinct stimulus bins. Then, the proportion of choosing category 'A' was averaged for stimuli within each bin. Notice that the proportion of choosing category 'A' is high for stimulus bins within category 'A' and low for stimulus bins within category 'B'. For both RB and II tasks, GCM's predictions matched the rats' behavior. b) These are the best fitting estimates for the attention weight parameters. The parameter estimates differed depending on the task type. Specifically, rats that had learned an RB task had high attention weights to the category-relevant dimension and low attention weights to the category-irrelevant dimension, suggesting that rats learned RB tasks by shifting attention to the category-relevant dimension. Conversely, attention weight estimates for rats that learned an II task were equivalent for both stimulus dimensions. Therefore, rats learning an II divided attention evenly. c-d) GRT was fit to the generalization data of rats that had learned an RB (c) or II (d) category task.³⁸ The gray points represent the stimuli presented during testing sessions, and each black line is the best fitting decision boundary for a single rat's data. Only a half of rats that learned an RB task were best fit by a uni-dimensional decision boundary (indicated by a line perpendicular to an axis). The other rats were best fit by bi-dimensional decision boundaries (indicated by a line with a slight slope). These results suggest that although rats shifted attention towards the relevant dimension, some attention was also allotted to the irrelevant dimension. d) All rats that learned an II task were best fit with bi-dimensional decision boundaries (indicated by sloped lines), suggesting that these rats divided attention between both dimensions. Data redrawn with permission from reference 38.

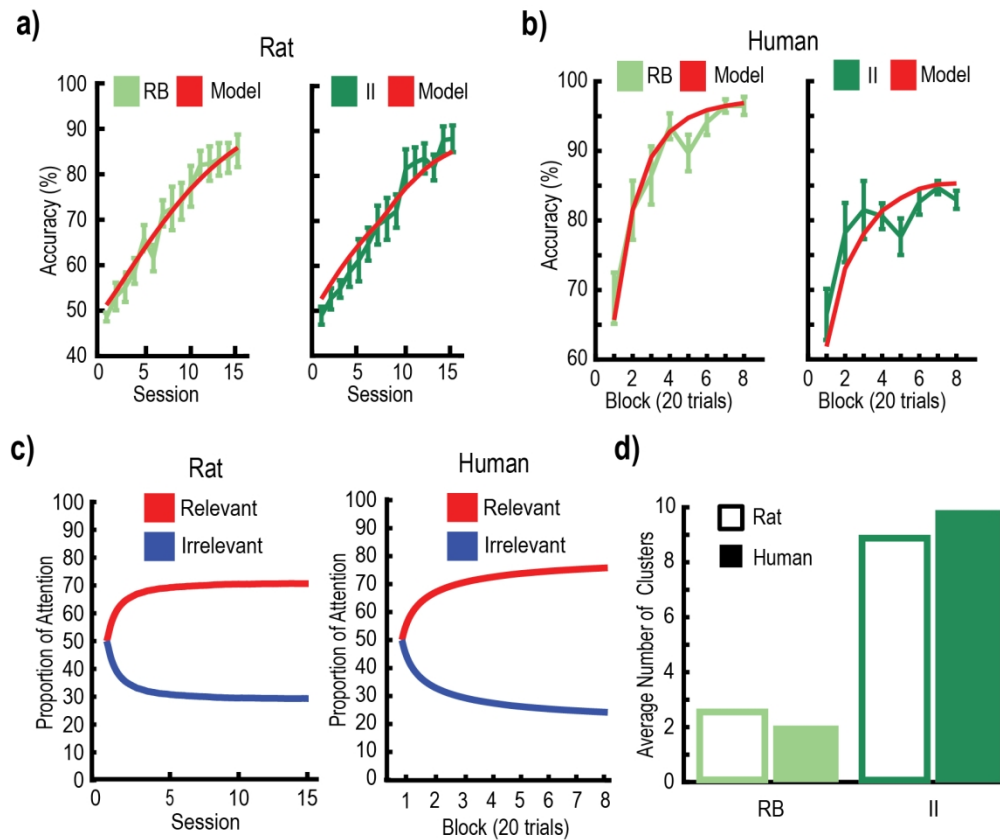


Figure 10. SUSTAIN, a neural network model of category learning, was trained to learn either RB or II categorization tasks. Then, SUSTAIN's predictions were optimized to the training data of rats (a) and humans (b). c) SUSTAIN can predict how attention is distributed between stimulus dimensions across training. Here, we plot SUSTAIN's estimated attention weights for rats (left) and humans (right) learning an RB task. Under SUSTAIN, attention is initially split between both dimensions, and then can make small adjustments after each trial. For both rats and humans, the attention weight for the category-relevant dimension increases across training (red line), and the attention weight to the category-irrelevant dimensions decreases across training (blue line). This suggests that both rats and human learn RB tasks by shifting attention towards the relevant dimension. d) SUSTAIN represents categories with one or multiple clusters, which represent previously experienced training exemplars. Making a category decision involves comparing the similarity between the current stimulus and existing clusters. SUSTAIN has a mechanism that recruits new clusters. This mechanism is flexible; therefore, the number of clusters that represent each category can vary. Here, SUSTAIN learned RB tasks by recruiting two clusters (one per category) and learned II tasks by recruiting multiple clusters (4-5 per category). This pattern was consistent when SUSTAIN was fit to both rat and human data and suggests that both species represent these category tasks similarly.