The color of objects adds relevant and sometimes critical information regarding the object at hand. Is a banana good? If it’s yellow, yes. If it’s green, no. But this information of course depends on what you’re looking at. Is red good? If it’s an apple, yes. If it’s your urine, no. (*previous sentence for private consumption only*). Thus, contingencies exist between objects and colors, with it often being the case that neither alone provides enough information to make an assessment of survival value. The brain must compute and remember these contingencies so survival value of environmental elements can be learned and recalled when needed.

To explore the neuronal structures and processes that underlie the formation and processing of color/shape contingencies in the brain, we set out to create a selection of stimuli that could be used to efficiently and meticulously elicit responses from neurons in brain areas where such contingencies are suspected to be represented. Of course, the selection of a stimulus space also requires consideration of the particular methods to be used in the application of such stimuli, and the questions that may or may not be answered by the techniques employed.

# Continuous Stimulus Space

To explore color/shape contingencies, we desired a set of colored shapes that would vary smoothly in both color and shape. That is, for every stimulus, there would be a similar stimulus differing only slightly in shape and/or color. Each colored shape would have a reward value associated with it, and nearby stimuli would be associated with similar rewards whereas stimuli that differ greatly might have very different reward values. We organized our stimuli into a two-dimensional space. To fill the requirement that both shapes and colors vary smoothly, we wished to avoid discontinuities along both the shape and color dimensions. This required that shapes and colors vary in a circular manner; as we sequentially go from one shape to the next, we would eventually end up with the shape at which we started.

# Circular color space

Color space naturally lends itself to a circular representation, with a proper choice of color space axes. While remaining in an isoluminant plane in color space, rotation through the hues at a fixed saturation and brightness yields a circular color space. The discrimination between similar colors is well established. It is straightforward to choose a circular sequence of colors similarly discriminable from each other. Colors are chosen in the *CIELuv* space at equal luminances, and equally spaced in the ***uv*** plane. As the will be presented on tablets in the monkey’s home cage during training, each tablet will be calibrated, and stimulus colors adjusted accordingly.



# Circular shape space

Shapes are not obviously organized into a space from which a circular representation can be derived. Thus, we compressed the multi-dimensional shape space into workable dimensions. Choosing shapes (exemplars) was done from a database of over 20,000 images. Each image had objects outlined by subjects during a psychophysical task, and each object was given a text label describing that object (for example: woman, boat, baby, flower, hand).

# Relevant axes

As we wish to explore color and shape contingencies in both primate behavior and in inferotemporal cortex (IT), we made use of a map of object space proposed by Bao et al. (2020) in which responses of neurons in IT varied gradually along across cortex along two axes describing particular object properties. They found that if stimuli were categorized according to blobbiness/spikiness and animacy/inanimacy, neurons in IT were spatially organized according to their responses to stimuli varying along these two categories. In anticipation of employing this map for both neurophysiological and fMRI studies, we also categorized our shapes along these two axes (spiky/blobby, animate/inanimate).

#### Animate/inanimate

Image outlines were rated by animacy by the interpretation of the labels placed on images by participants. When traced, each shape was given one or more labels according to the object being traced (as described above). Additionally, we assigned each label an animacy rating on a scale of 1-6. (Gallant?) This produced an animacy score from 1-6 for each image outline, with 1 being least animate (a hammer, for example) and 6 being most animate (such as a child playing).

#### Spiky/blobby

To evaluate spikiness/blobbiness, outlines were quantitatively processed to get a spikiness metric. We quantified four characteristics for each outlined shape: the outline perimeter (PS), the outline area (AS), the perimeter of the outline’s convex hull (PC), and the area of the convex hull (AC). From these numbers, we determined a rough estimate of convexity C = As / Ps. In addition, we calculated a measure of roundness, as longer shapes might be considered more spiky than rounder shapes. Roundness R = Ac / Pc. Using these factors, we arrived at an appropriate measure of spikiness/blobbiness that matched our qualitative assessments:

Spikiness = 1 - Sqrt([C 2+ R2]/ Ac)

## 

## Interpolating shapes

### We wanted to create a shape space that varied circularly, like the color space, with each shape similarly distinguishable from nearby shapes. We started by plotting each shape with its spikiness versus its animacy. (show) We chose four exemplars from each of the four corners (animate/spiky, animate/ blobby, inanimate/blobby, inanimate/spiky). Each shape is simply a closed black outline.

### Adobe Illustrator

### In Adobe Illustrator, we used the Blend Tool to create 360 total shapes from the four exemplars. We interpolated 89 shapes between each adjacent pair of exemplars to yield 360 unique shapes, varying smoothly between exemplar pairs.

### Amazon Mechanical Turk

### Although the shapes varied smoothly and equally in terms of algorithmic blending, we required adjacent shapes to be similarly perceptually discriminable (needs explanation). To do this we presented shapes to human subjects using Amazon Mechanical Turk (AZMT). Using sets of 36 shapes at a time, we refined the set of 36 shapes over several iterations until the psychophysical results approximated a circular space with similar perceptual differences between adjacent shapes.

Each iteration used 36 unique shapes from the 360 shapes generated. The first iteration used every 10th shape (i.e. shape 1, 11, 21, …, 351). On each trial, subjects were presented with three shapes and asked to choose the shape that was least like the other two: an odd-one-out task. Responses were used to populate a dissimilarity matrix, with each response adding to two elements of the matrix.

To exhaust the total number of possible comparisons, the number of required trials was 36 choose 3, or 7140 trials. We added a number of catch trials in which two of the shapes were identical. These trials were used to gauge the reliability of the subject’s responses. Failure to choose the odd stimulus on these trials indicated that the subject’s responses were not to be trusted and should be discarded. We added 860 catch trials to the 7140 required to bring the total to an even 8000 trials (catch trials comprising 10.75% of total trials). We required subjects to respond correctly on 85% of the catch trials, as we realized that the odd one out on catch trials would occasionally be very similar to the two other shapes.

To complete 8000 trials at an estimate of 2 seconds per trial would take almost 4.5 hours. We therefore divided the 8000 trials into 20 chunks, each of which could be completed in under 15 minutes. Trials were randomized before dividing into the 20 chunks. Catch trials were generated randomly, and an equal number of catch trials was added to each chunk. Each set of trials was again scrambled to randomly interleave the catch trials.

## Iterative convergence on circular shape space

Initially, we started with one exemplar and chose every 10th shape, for a total of 36 shapes including each of the 4 exemplars. Workers on Amazon Mechanical Turk (AZMT) populated a dissimilarity matrix, in which each element represented a shape/shape comparison. Each decision by each worker incremented the dissimilarity count between the chosen odd shape and its two alternatives. We usually required that the 8000 comparisons for each set of 36 shapes be presented at least four times (32,000 trials total) before analyzing the results. Each element in the finished matrix contains the number of times each shape was deemed dissimilar from each other shape.

#### Perceptual distance

The dissimilarity matrix was then processed using Matlab’s **mdscale** to produce a multi-dimensional scaling (MDS) representation of shape/shape comparisons, in effect yielding a two-dimensional map of the perceptual “distances” among all shapes.

#### Circular organization

The goal was to create a circularly sequential set of shapes in which each shape is most similar to its adjacent shapes in the sequence, and each shape is equally discriminable from the next shape in the sequence. In addition, we wanted shapes that were not near each other in the sequence to be judged dissimilar. We therefore wanted to converge on an equally-spaced circular organization of shapes in the multidimensional scaling representation of the dissimilarity judgments. We would expect the shapes in an MDS representation to be equally distant from the origin, and equally spaced among themselves (10° using 36 shapes).

Given the results of an AZMT experiment (in which we achieved a reasonable account of shape/shape comparisons), we determined how far the MDS representation of the data deviated from our desired objective. A simple measure of how circular our results were was obtained by multiplying the standard deviation of the angular distances between shapes in the MDS space by the standard deviation of their distance from the origin. This would of course be zero for a perfectly circular space.

#### Choice of next iteration

We required a method of choosing new shapes from the distances measured in the MDS representation of the previous set of shapes. Given the angular positions of the shapes in the MDS, we took each pair of shapes and linearly interpolated their interim shapes (the shapes falling between them in the original set of 360) between the pair of shapes. For example, if shape #60 was at 55° and the next shape #75 was at 85°, we would place shapes #61-#75 every two degrees so that all shapes #60-#75 evenly spanned 55°-85°. Then, beginning with shape #1 at 0°, we chose the shape closest to each 10° division around the circle. From the previous example, this would mean choosing shapes #63, #68, and #83 for the 60°, 70°, and 80° positions, respectively. This process gave us 36 new shapes that we again put into AZMT as described above. We did this for six iterations, achieving a somewhat circular, evenly spaced organization of shapes.



#### 

Iteration

#### Resulting space and compression of characteristic axes

Interestingly, the resulting shape space did not evenly represent shapes between the four exemplary. An even representation would entail eight interim shapes between each pair of exemplars. The psychophysical organization of the shapes resulted in far fewer shapes along the animacy axis than along the spiky axis, indicating that spiky and blobby shapes are more perceptually similar among themselves than are animate or inanimate shapes.



# Conditional Reward Space

Our stimulus space attributed a reward value to each shape/color combination. By assigning ordered shapes along the Y axis and ordered colors along the X axis, we placed reward values within the resulting two-dimensional space such that similar stimuli would have rewards that varied slightly, but very different stimuli could have very different rewards.

We had several requirements for our stimulus space. First, we needed stimuli to have reward values that could not be predicted by color or shape alone. That is, subjects would need to learn color/shape contingencies to maximize rewards. This meant that, in the stimulus space described above, reward values would be oriented in this color/shape stimulus space.

## Oriented Gaussian Reward Bases

To vary reward values smoothly, we used 2D Gaussians to represent stimulus value in the 2D stimulus space. After exploring several parameter options, we settled on eight 2D Gaussians. We implemented the Gaussians using Matlab’s **mvnpdf**. Gaussians had an X/Y SD ratio of either 5/1 or 1/5, with a covariance of 0.85. These parameters were chosen after evaluating multiple randomly generated spaces.

Note that as the shape space and the color space were designed to be circular, the shape space was designed to be circular along both axes.

We desired optimal performance in our stimulus space to require the use of color/shape contingencies. Using either color or shape should provide far fewer rewards than recognizing the value of color/shape combinations. We therefore required a large difference between the rewards given by employing color/shape contingencies and the rewards given by choosing stimuli based on either of the marginals (color value or shape value alone) or even using both marginals (the independent combination of color value and shape value).

We also wanted both stimulus color and stimulus shape to provide useful information. That is, using the information provided only by shape should provide more rewards that simple chance. Likewise, using color should do the same. Furthermore, using shape and color together, albeit independently, should do even better. Finally, greatest rewards would be obtained by recognizing the relationship between color and shape and using those contingencies.

### Space selection

We consequently developed several metrics which would aid in our choice of space. For both color and shape to independently provide useful information, we required the shape and color marginals to not be flat. Flat marginals would be penalized more than more variable marginals. A flat color marginal would value all colors the same.

One way to do this was to penalize marginals with many low values in their first derivative. We therefore assigned an error function to each marginal (shape and color). We calculated a desired minimum derivative (difference) between adjacent elements. If N is the number of shapes or spaces on the marginal, the minimum derivative was defined as 1/(10\*N^2). Each marginal error was simply the marginal reward difference between adjacent elements that fell below this minimum value. Flatter marginals would have a higher number than more variable marginals.

(above could be calculated better. It worked at the time as a quick solution, but I’m sure I can do better without changing the results)

The probably more important metric was maximizing the difference between marginal and contingent rewards. That is, maximizing the difference between the rewards that could be obtained by using color and shape independently, and rewards from using both shape and color in a contingent manner.

Such a metric would of course be dependent on how stimulus value is converted into reward. We implemented a discrete reward scheme that had four tiers, ranging from 0 to 3, with 0 being least desirable, and 3 being most desirable. The reward value for each stimulus is discretized by assigning each of the four discrete values to increasing ranges of values in the stimulus space. After normalizing stimulus values in the 2D space from 0-1, we imposed four reward tiers in the ranges 0.0 - 0.01 - 0.1 - 0.4 - 1.0. Although somewhat arbitrary, these ranges were chosen after examining many stimulus spaces with both high and low minimization errors, and were chosen to qualitatively equalize stimuli with and without rewards. (we could quantify this and use it in choice of which space to use).

After calculating discrete reward values for the stimulus space, we did the same thing for the reward space predicted by using the marginals dependently. We calculated the difference between the reward space and the marginal prediction of the reward space. We multiplied the sum of all these values by the same epsilon used in the marginal error (1/(10\*N^2)).

The total error to be minimized was calculated as the product of the three individual errors (x-marginal, y-marginal, reward space).

We wished to be able to generate several unique stimulus spaces so we could ultimately test different groups of animals on different shape/color contingencies. This would help insure that later results are not an artifact of the particular stimulus space chosen. Traditional error minimization tended to produce remarkably similar spaces, as would be expected in the absence of distant local minima. We therefore chose a Monte Carlo method to produce our stimulus spaces. In effect, we generated thousands of stimulus spaces, and chose as candidates those with the lowest errors.

In addition to the stimulus space determining reward, we also wanted a space to determine the frequency at which each stimulus appeared: the prior. Not all color/shape combinations would appear equally as often. The procedure for generating the frequency space for stimuli was almost identical to that of the rewards. The only difference is that we increased the spatial extent of the Gaussians by 250%, to provide a greater probability of nearby stimuli appearing independent of reward value. We wanted a greater chance of nearby stimuli being presented regardless of their value. Thus we made the spread in stimulus probability greater than the spread in reward value.

**Simulations.**

Once we obtained candidate spaces determining stimulus reward and stimulus probability, we ran several simulations of learning the stimulus space to explore the best number of stimuli to present during training. We began with a neutral stimulus space representing the value assigned to each stimulus. We added a small amount of random noise, so there was no systematic bias in the beginning simulation state. There were three primary parameters in our simulations. The first was the number of stimuli presented during each trial. For each trial, a number of stimuli were choses according to the frequency space being used. The second was a perceptual error modeled as a 2D circular Gaussian. This added similar perceptual noise to identification of the shape and the color. The stimulus perceived was chosen using the Gaussian centered at each presented stimulus. The simulated subject now had a number of perceived stimuli, and would always choose the perceived stimulus associated with the greatest reward in the stimulus space. Given the reward associated with the chosen stimulus, the shape space representing stimulus value was updated using a second 2D Gaussian centered on the perceived stimulus with an amount proportional to the reward value. The simulated subject’s error was simply the difference between the actual stimulus space and the learned stimulus space normalized by the total number of stimuli in the space.

Plotting error versus time, the resulting curve was fit well with a normal PDF centered near time zero. We therefore fit each learning curve (error over time) to a normal PDF parameterized by a mean (which was held near zero), a standard deviation (representing learning rate), a Y offset (representing the asymptotic lowest error attained) and a scale (representing the range of errors). We were primarily interested in rate of learning (standard deviation) and minimum error (Y offset).

Across all parameters, learning time and minimum error decreased with the number of simultaneously presented stimuli, and were at or near their best values when the number of stimuli reached 4. Although the number of stimuli during training was not particularly critical, these results indicated that no fewer than 4 stimuli should be presented at once.

|  |  |
| --- | --- |
| Error |  |

# stim

The final error from each simulation is plotted as an open circle in the above plot. For each number of simultaneously presented stimuli, results are included across the other parameters (perceptual noise, breadth of generalization during learning)

**Post-hoc criteria**

Given our stimulus spaces determining stimulus value and stimulus frequency, we applied some post-hoc criteria to optimize our choice of stimulus space. We wished our choice of stimuli in each trial to be entirely a function of the determined frequency space. As many stimuli would be associated with no or negative rewards, it is clear that a certain percentage of trials would contain stimuli with no reward. This percentage decreases with the number of stimuli presented per trial, but is non-zero nonetheless. Using the previously determined number of four stimuli per trial, we again ran simulations in which we randomly chose 4 stimuli (with repetition) according to the frequency space. Over thousands of trials, we totaled up the number of trials in which no stimulus was associated with a positive reward. We believed that trials with no reward would tend to discourage the subject, so we sought to minimize spaces that produced a large proportion of no-reward trials. Our goal was to keep this proportion below 10%. *I’m going to go with 10%, although the spaces we choose will probably be lower than that. Just describing the candidates.*

The second post-hoc criterion addressed the variety of reward vs. frequency. We wished for high valued stimuli to be both frequent and infrequent, and we desired the same thing for low-valued stimuli. We quantitatively examined stimulus spaces in two ways. The first was to visualize the reward space overlayed on a contour representing stimuli presented more than 40% of the time. We checked to be sure each reward tier was sufficiently represented for stimuli above and below 40% presentation frequency.

Similarly, we plotted the frequency at which each reward appeared in the space, and ensured the frequency distributions were similar.

**(Post-hoc criteria can certainly be quantified and put into minimization)**

Again, these two are qualitative, but can easily be adapted to quantitative criteria. Or they can be omitted entirely if deemed not necessary.

**Training:**

In the initial phase of these experiments, monkeys will be trained on the stimulus space to hopefully learn the particular shape/color contingencies. First, however, the young monkeys must be trained to touch the tablet, and must be trained that touching the tablet provides reward. This is accomplished by presenting a single salient stimulus on the screen: a large dark/light checkerboard with the same mean luminance as the grey background, with a Gaussian contrast profile (fades at the edges). Monkeys will quickly learn to touch the screen and receive juice. It will be critical for the monkeys to be on water control at this point in order for the dispensed juice to contain actual reward value besides that of novelty.

Once the monkeys are reliably touching the screen to obtain reward, we will begin the proper training. Each trial will begin with the same Gaussian checkerboard used in the first stage. Upon touching the screen, the checkerboard will disappear and four stimuli, chosen at random (duplicates allowed, as the chance of a duplicate is less than 0.5%) using the frequency space, will appear at equal separation around the center of the screen. Upon touching one of the stimuli, the consequence associated with that stimulus will occur. We will incorporate a four-tier reward system, dictated by the four-tier reward space implemented above. We shall call these tiers 0, 1, 2, and 3, going from least desirable to most desirable. Tiers 2 and 3 will be small and large juice rewards, respectively. The difference between the two positive rewards will be significant. Reward tier 1 will be no reward. Reward tier 0, the least desirable, will initially consist of a time-out, during which the monkey must wait a certain amount of time before the experiment resumes. We will couple the time-out with a buzzing or beeping which will add to the disruption of the experiment due to a poor choice.

Although colors will be chosen to be all at the same brightness for a given tablet screen, it is possible that environmental lighting or differences between individual monkeys could cause slight differences in the perceived brightness of different colors. This may render some colors perceptually brighter or darker than the background. To prevent the monkey from using any perceived luminance differences rather than the hue of the color, each color used will be presented at a range of different luminances (probably 5 above mean and 5 below mean, over a range that is +/- 15% luminance contrast computed by Weber contrast) that will be selected according to a normal distribution centered on the canonical luminance determined for each color.

Results will be monitored daily to track learning progress, as the frequency of stimuli chosen approaches the structure of the stimulus space. As there are 36x36 or 1296 stimuli and all are not sampled equally, it is unlikely for any single day’s data will provide meaningful results; data will have to be pooled over days to properly track progress.

Alternatively, we may initially start with a single stimulus, as the monkeys may not learn to direct their touch choices if simply slapping the screen always does something. They must learn to select objects rather than just touch the screen.

We will track the progress of each monkey as they learn the stimulus space. If behavior converges on a space very different from the original reward space, these results will be examined for systematic issues that might be addressed by changing the training regime.

SPECIFIC TASK

**Experiments:**

Once the monkey’s behavior converges on the original reward space, we can then probe their representation of this space to answer questions about color and shape dependencies.

Given the continuous nature of our stimulus space, we have the ability to subsample the space to speed up data collection to obtain an overview, and the ability to examine the structure of the monkey’s learned space at a finer resolution by introducing stimuli between those in the stimulus space. While conducting these experiments, the monkeys will also continue the training paradigm to continually reinforce the learned space, and to hopefully eradicate any inconsistencies they may experience during the experiments.

**Psychophysics**

**Alternate shape spaces**

One question that could be answered by psychophysics is if color contingencies generalize to the stimulus characteristic axes proposed in IT (spiky/blobby, animate/inanimate). We can construct another circular shape space by choosing different exemplars from the large set of traced shapes. We would again plot the shapes by spikiness/animacy, but choose four different exemplars from the corners of the space. We then create a new circular shape space using AZMT. Although the original and new shape spaces may not align exactly at the four exemplars, we will be able to associate shapes with equivalent or at least similar spiky or animate characteristics between the two spaces. By taking the angular theta value of each shape in the circular shape space, we can associate a spiky/animate value pair to each angle. We then take the spiky/animate values of the new shapes and assign them appropriate locations along the shape axis of the original reward space, giving us a new stimulus space using novel shapes that rewards animacy and spikiness similarly to the original space.

To probe the alternate shape space, we will modify the training paradigm to include a certain proportion of probe trials in which all four stimuli are drawn from the new stimulus space. We realize that over time the new shape/color combinations will eventually be learned by the monkey, but given the size of the space and the learning curve of the original space, we are certain that initial results on probe trials will not reflect learning of the new stimulus space.

Choosing novel shape/color stimuli in a manner consistent with the spikiness/animacy of the original learned shape will suggest that these characteristics are generalized across shapes when assigning value to shapes according to their color.

**Are marginals extrapolated?**

How is value now placed on a shape in the absence of color? Do the monkeys actually extrapolate the shape marginal, or is shape choice influenced by either of the other stimulus factors (color, frequency)?

We would present shapes without color information. As we used colors at varying luminance for the training, monkeys will hopefully have learned to decouple luminance information from hue information in the color space. Therefore, using a mean grey fill for the shapes should not cause the monkeys to associate that mean grey with one color over another. Also, using mean grey as a shape fill will make the shapes appear as black outlines on a uniform mean grey background rather than as outlines filled with a particular color.

To solve the issue of how to reward trials during this experiment, we would present two shapes from the stimulus space along with two novel neutral (in terms of spiky/animate) shapes. The two shapes from the original stimulus space would be rewarded equally, whereas the novel neutral shapes would give no reward. Responses to the novel shapes would act as a control to indicate the level at which the monkey is actually reporting learned shape value. Analyzing the frequency at which shapes are chosen will provide us with a measure of the monkey’s marginal preference for shape in the absence of color.

In addition, deviation from the marginals predicted by the reward space can be analyzed in terms of color and stimulus frequency. A tendency to choose a shape, for example, that was not the most valuable shape as predicted by the marginal can be examined in the context of the stimulus space to see if this tendency could be explained by the structure of the reward space, being influenced by either color preferences or the frequency of the shape appearing, or even interactions between the color and frequency.

**Electrophysiology**

We hope to explore whether any aspects of learned color/shape contingencies are present in the responses of neurons in IT. The experiments described will focus on single cell recordings, but multi-unit experiments are certainly a future possibility.

Each experiment will start with an initial characterization of each isolated neuron’s responses. After a qualitative determination of receptive field (RF) location and extent, we would obtain both color and shape tuning curves with the colors and shapes that define the learned stimulus space.

Depending on the neuron’s responses to shapes and colors, a subregion (or subregions) of the stimulus space can be chosen for greater examination. The best choice would be a region of the stimulus space in which the neuron responded selectively to colors and/or shapes, and in which the rewards require color/shape contingencies (the rewards are oriented in the stimulus space). Using the shapes and colors that specify this region, we would obtain a matrix of responses for all stimuli in this region. Again, we can either sub sample or interpolate shapes and colors for probe larger or smaller regions of the space, respectively.

A response matrix can be viewed as either a set of shape tuning curves at different colors, or as a set of color tuning curves for different shapes. Either way, analysis can show if and how the tuning curves change along the other axis.

We can also present the novel shape space to IT neurons once the shape and color tuning characteristics have been determined. Even if responses to the original shape set are sparse for a neuron, we could test with the secondary shape space. If there are substantial responses to shapes in the secondary space, similar curves can be obtained to check the existence of any color/shape contingencies in neuronal preferences, and whether these contingencies relate to the learned shape space.

Should responses change in accordance with the reward space, this would suggest that color/shape contingencies exist in the activity of IT neurons. If responses to stimuli are separable into their color and shape responses, this would indicate that color/shape contingencies are coded somewhere after IT in the processing stream.