Attentive Surround Suppression in the Feature Dimension

Xin Chen and John K. Tsotsos

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Department of Computer Science and Engineering
4700 Keele Street, Toronto, Ontario M3J 1P3 Canada

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Xin Chen
Brain & Behavior Discovery Institute,
Georgia Health Sciences University
xchen@georgiahealth.edu

John K. Tsotsos
Department of Computer Science & Engineering,
York University
tsotsos@cse.yorku.ca

Abstract

According to the selective-tuning model (Tsotsos, 1990), attending to an feature value results in an surround-suppression on close feature values, but not for feature values farther away from the attended one. To validate this prediction, subjects were first required to attend to an orientation (or color) value, and then their perception of other orientation (or color) values, which could be at, near, or far from the attended feature value, was probed. In line with this prediction, the results revealed that in both orientation and color domain, attending to a point in the orientation (or color) domain results in a surround-suppression for close orientations (or colors).

Introduction

It is a commonly held position that attention is needed to deal with enormous quantity of information our eyes see (Broadbent, 1956) and more importantly with the combinatorics of how it may be perceived (Tsotsos, 1990). A vast array of potential models and theories have arisen that attempt to explain attention in this context (Itti, Rees, & Tsotsos, 2005; Rothenstein & Tsotsos, 2008). Virtually all models focus on the large number of locations at which items of interest may be found in the visual field and all models provide proposals on how selection in the spatial dimension may take place. However, is this the only source of the problem of too much data and too high combinatorics of perception? One model, the Selective Tuning (ST) Model (Tsotsos, 1990; Tsotsos et al., 1995) proposes that there are other sources as well, one of them being the feature dimension. That is, not only must our perceptual systems choose among the many possible locations where relevant stimuli may be found, but because the visual system decomposes visual input into a huge number of feature values, computed automatically at each position, choices there can also impact the efficiency and efficacy of the overall process. Here, a single feature is defined to be a single neural tuning, that is, a band-pass filter centered at one value in some feature dimension (color, orientation, velocity, disparity, etc. - see Wolfe (1998) for a list of pre-attentive features that elicit attention), and at one scale, centered at one location in the visual field. In other words, it is not enough to simply choose among locations when at each location hundreds of features are computed, many perhaps not relevant to the task at hand. In the same way that other locations are not relevant and ignoring them leads to less computation, ignoring irrelevant features also contributes to reducing the computational load of perceptual processes.

The ST model has predicted that attentive selection occurs in the feature dimension as well as in location. The effect is very specific and is based on suppression in the neighborhood of the attended item. Neighborhood here is defined as the set of feature values that are 'close' in the dimension of interest: orientation, color, depth, etc.

In the ST model, one important reason for surround suppression is that it provides a solution to the Context Problem (Tsotsos, et al., 1995). The Context Problem simply states that in a neural network where there is a feed-forward convergence of neural signals onto a single neuron, any stimulus present in the set of afferents to that neuron exists within the context formed by the set of those afferents as a whole. The most direct manifestation of this is that any stimulus in an input image has a spatial context. A stimulus close to the attended one will also be an input to that same neuron and thus there is ambiguity as to what that neuron's response might mean (Reynolds & Desimone, 1999). However, because of the band-pass nature of any neuron's tuning properties, there is context in feature dimensions as well. At the same location, there are many band-pass feature neurons and many respond to some degree to a single feature at that location and each provides feed-forward inputs to neurons at the next layer in a network. In effect, this is a population response problem; in order to enable more efficient coding more than one neuron responds to any given stimulus. In the spatial dimension, a threshold on retinotopic distance suffices to make the notion of nearby precise. In the feature dimension, a close feature is one that elicits a similar response from the neuron tuned for it, within some bound. The result is that there is a greater potential for ambiguity at subsequent processing layers. Attention provides a solution to this problem by suppressing the most problematic responses.

It is important emphasize that the mechanism in ST is a top-down one, not a lateral cooperation mechanism. Suppose the tuning curves for feature neurons—for color—are as shown in Figure 1a. The figure illustrates a classic conception of a Gaussian-like tuning profile for each of 15 neurons, each tuned to a particular hue. Figure 1b shows what the overall response of this population of neurons might be for a stimulus of the central hue value, red. A search for the position of the peak of this population response suffices to permit the correct detection of that feature. Noise may make this more difficult, however. Small amounts of noise could easily cause that largest response to be a bit smaller while increasing a neighboring neuron's response just enough to surpass it - thus leading to an erroneous conclusion. Consider what happens if the population as a whole is tuned for red by suppressing neighboring hues, as shown in Figure 1c. The response from the neighboring neurons in the hue dimension is suppressed and, along with it, any responses due to noise in the stimulus from those neurons. As a result, the detection of the correct peak is facilitated. The magnitude and extent of suppression would dictate the amount of improvement. The difference between the overall population response in Figure 1b and the attended response of Figure 1c (shown in light gray for comparison) exhibits the familiar Difference of Gaussians profile. This neighboring feature suppression is the analogue to the spatial surround suppression described earlier and points to the fact that there is a Context Problem in feature space to contend with as well. Moreover, as is evident in Figure 1c, the tuning curve of the overall population is sharpened toward the attended hue, as (Haenny & Schiller, 1988) and many others since have shown.

Following up on a previous positive study (Tombu & Tsotsos, 2008) that demonstrated attentive feature suppression the orientation dimension, we describe new experiments that test attentive feature surround suppression using a pre-cue paradigm in both orientation and color feature spaces. We observed that orientations or colors close, in orientation or color space, to the attended one are suppressed, but not orientations or color farther away in feature space (respectively). This supports the ST prediction of attentive surround suppression in the feature dimension and experiments testing this for other feature dimensions are in progress. We note that evidence for attentive surround suppression in motor space has recently been presented (Loach, Frischen, Bruce, & Tsotsos, 2008) strengthening ST's overall position on this issue.

Experiment 1

ST predicts that attending to a specific orientation will resulting in an inhibition ring around that orientation in orientation space: only close orientations will be inhibited but not the farther away ones. To test this prediction, we adopted an orientation pre-cue paradigm inspired by Posner’s (1980) spatial pre-cue paradigm. A pre-cue orientation was used to attract the subjects’ attention to a particular orientation. And then the subjects’ perception of orientations of various values was probed. We expected that the perception of orientations close to the cues would be deteriorated, but not the orientations farther away from the cues. In the current experiment, there was also an orientation distractor immediately following the cues, for the purpose of forcing the subjects to attend to the cue by presentation of distractors.

Method

Participants

Ten subjects participated in this experiment. All the participants were students or staff from York University and have normal or corrected to normal acuity and color vision. All procedures were approved by York University's Human Participants Review Sub-Committee (#2008-219).

Stimuli and Apparatus

The stimuli, same as those used by Tombu and Tsotsos (2008), were striped circular disks oriented at different directions. The disks had a radius of 180 pixels, and 36 stripes per disk. Stripes were of alternating light and dark gray on a medium gray background. The stripes on the disks could be either straight or jagged (see Fig.2A). All stimuli were presented on a 19 inch CRT monitor with a screen resolution of 800 × 600 pixels and a refresh rate of 85 Hz. The viewing distance is approximately 36 cm, creating a view of 53° (H) × 41° (V), and the radius of the discs are about 6.5° visual angle. Manual responses were collected by using a Microsoft SideWinder gamepad which was connected to a USB port on the computer. Custom C++ software incorporating DirectX functionality and running under Microsoft Windows XP was used to control the experiment.

Procedure and Design

The experiment presentation sequence was as Fig.2B. Each trial started with a central fixation point. And then an orientation cue presented for 100 msecs, followed by a mask for 50 msecs, and then followed by an orientation distractor, which was always 45° different from the cue, for 100 msecs, and then followed by a mask for 166 msecs, and then a probe orientation presented for 150 msecs, followed by another mask for 166 msecs. Finally a fixation point was presented again while waiting for the participants to respond. The participants were instructed to press the left-trigger of the gamepad if the stripes on the probe stimulus were straight, or right-trigger if they were jagged. Feedback was displayed for 1000 msecs after the participants' response. A 200 msecs 2000 Hz tone would signal the incorrect responses. The duration of the cues and probes were determined by pilot experiments. And the 416 msecs stimulus onset asynchrony (SOA) between the cues and the probes would give orientation attention enough time to engage. The orientations of the cues could be any angle of 0° ~ 180° (but without angles of <10° close to horizontal or vertical) randomized on a trial-by-trial basis. The probes would be at the same angle as the cues for 66% of the trials. For the rest of the trials, the probes were different from the cues by 5° (6.6% of the trials), 10° (6.6%), 20° (6.6%), 45° (6.6%) or 90° (6.6%). Each participant had to run at least 10 blocks, and each block has 180 trials.

Result and Discussion of Experiment 1

The dotted line in Fig.3A is the curve of the subjects' sensitivity d′ collapsed over different probe conditions. Apparently the orientation perception was inhibited when the probes were 10° or 20° close to the cues. A one-way repeated-measures ANOVA confirmed our observation: the probe conditions had a significant effect on the subjects' sensitivity d′, $F(5, 45) = 3.87$, $p = 0.005$. And further paired Student's t-test revealed that the subjects' d′ under probe 10° condition was significantly less than 0° ($t = -2.48$, $p < 0.02$), 5° ($t = -2.30$, $p = 0.02$), 45° ($t = -2.65$, $p = 0.01$), 90° ($t = -2.64$, $p = 0.01$); and also the subjects' d′ under 20° condition was significantly less than 0° ($t = -2.63$, $p = 0.01$), 5° ($t = -2.57$, $p = 0.02$), 45° ($t = -4.92$, $p < 0.01$), and 90° ($t = -2.60$, $p = 0.01$). However, probe 10° and 20° conditions were not significant different, $t = 1.32$, $p = 0.22$.

The experiment does not permit conclusions for surround-suppression of orientations from 10° to 20° close to the attended one. Fig.3B shows the individual subject's d′ under different probe conditions. Unlike cross-subjects average curve, individual subject's orientation perception was suppressed on the probes of either 5°, 10° or 20° away from the cues, but not all or any two of these conditions. Therefore the surround-suppression could occur at 5°, 10° or 20° close to the attended orientation, depending on individual differences.

ST's prediction on orientation attention was confirmed. However, Tombu and Tsotsos (2008) found that the surround-suppression occurred around 45° away from the attended orientation. This difference could be attributed to several factors, such as, they only probed the attention inhibition at 0°, -45°, 45°, or 90° away from the attended one, and did not probe the 5°, 10° or 20° conditions. They also used a paradigm different from our pre-cue paradigm. In experiment 2 we addressed the question whether or not the presence of distractors after the cues changed the attention's gain or tuning properties and therefore resulted in the difference between ours and Tombu and Tsotsos's (2008) findings?

Experiment 2

In this experiment we modified the paradigm of experiment 1 by eliminating the distractor presented right after the pre-cues. We were interested in seeing what the effect would be after removal of the distracters, and whether or not the suppression might flatten or be shifted.

Method

Participants

Nine subjects participated in this experiment. All the participants were students or staff from York University and have normal or corrected to normal acuity and color vision. All procedures were approved by York University's Human Participants Review Sub-Committee (#2008-219).

Stimuli and Apparatus

Same as in experiment 1.

Procedure and Design

The stimuli sequence was as follow (see Fig.2C): each trial started with a fixation point on the center of the screen, and then the orientation cue was presented for 200 msecs, and followed by a mask for 166 msecs. Then the probe orientation was presented for 150 msecs, and followed by a mask again for 166 msecs. Except for the fact that there were no distractors, anything else was same as in experiment 1.

Result and Discussion of experiment 2

The solid line in Fig.3A shows the curve of the subjects' d′ collapsed on different probe conditions. The subjects' orientation perception was suppressed when the probes were 5° or 10 ° away from the attended orientation, and it was confirmed by a one-way repeated-measures ANOVA, $F(5, 40) = 3.35$, $p = 0.012$. Further paired Student's t-tests revealed that subjects' d′ under 5° condition was significantly less than 0° ($t = -2.79$, $p = 0.01$), 20° ($t = -2.99$, $p = 0.008$), 45° ($t = -1.65$, $p = 0.06$), but not for 90° ($t = -1.14$, $p = 0.14$). Also the subjects' d′ under 10° condition was also significantly less than 0° ($t = -2.51$, $p = 0.02$), 20° ($t = -2.49$, $p = 0.02$), 45° ($t = -3.55$, $p = 0.004$), and 90° ($t = -2.74$, $p = 0.01$). However, paired Student's t-test did not find significant difference between 5° and 10° conditions, $t = 0.55$, $p = 0.60$.

Fig.3C shows the individual subjects' d′ on different probe conditions. Once again, inhibition occurred close to the attended orientation, and could be as close as 5°, 10° or 20° from the attended orientation, depending on individual differences. Therefore similar inhibition patterns appeared regardless of the presence or absence of distractors. The difference between our experiments and Tombu & Tsotsos (2008) could not be attributed to the presence of a competing distractor and is thus more likely due to their coarser sampling in orientation space. However, we noticed that the subjects' overall sensitivity decreased with the removal of the competing distractors. This may suggest that distractors increased attentional gains, though did not changed the attentional tuning properties.

Experiment 3

In experiment 1 & 2 we confirmed the existence of attentive surround-suppression in the orientation dimension. ST's prediction was made for feature attention broadly, not only for orientation attention. Considering the possibility that different features could have different attention mechanisms, for example, Theeuwes (1992) demonstrated that color-defined singleton distractor interfered with the shape-defined feature attention, but not vice versa, we decided to extend our investigations to color attention.

Method

Participants

Ten subjects participated in this experiment. All the participants were students or staff from York University and have normal or corrected to normal acuity and color vision. All procedures were approved by York University's Human Participants Review Sub-Committee (#2008-219).

Stimuli and Apparatus

Colored striped circular disks were created, similar to the disks used in experiment 1 & 2. However, this time the stripes of the disks are of alternating color and dark gray on a medium gray background. Since orientations are no longer of interest, all discs were constantly oriented at 70° at this time. The color strips could be any of 180 colors. These 180 color have same saturation value, but have different hue values determined by equally dividing the HSV color wheel into 180 units.

Procedure and Design

The experimental procedure was same as in experiment 2. Only this time the color, but not orientation was manipulated. The pre-cues could be any of the 180 colors randomized on a trial-by-trial basis. The probes were same color as the cues for 66% of the trials. For the rest of the trials the probes hue could be 5, 10, 20, 45, or 90 units different from the cues, the smaller the difference the closer to the cues in color space.

Result and Discussion of Experiment 3

Fig.4A represents the subjects' sensitivity d′ under different probe conditions. The suppression occurred when the probe's color hue was 20 units away, according to the HSV color wheel, from the cue's hue. A one-way repeated-measures ANOVA was significant: the probe's color hue had a significant effect on the subjects' sensitivity d′, F (5, 45) = 5.96, p <0.001. We compared probe 20 condition with all other probe conditions by paired Student's t-test, and found that the subjects' sensitivity under probe 20 condition was significant less than probe 0 condition (t = -2.79, p = 0.01), 10 condition (t = -2.45, p = 0.02), 45 condition (t = -2.05, p = 0.04), 90 condition (t = -3.25, p = 0.005), but not significant less than probe 5 condition (t = -1.56, p = 0.08). Fig.4B presents the individual subject's sensitivity d′ under different probe conditions. Again, the individual subject's perception was either suppressed under probe 5, 10, or 20 conditions, respectively. Therefore we successfully extended our findings of center-surround suppression, with its individual differences, from orientation attention to color attention.

Conclusions

Attentional modulation suppresses potentially confounding stimuli within a receptive field. This was predicted in Tsotsos (1990) and has now received experimental support from other researchers (Bahcall & Kowler, 1999; Boehler, Tsotsos, Schoenfeld, Heinze, & Hopf, 2009; Caputo & Guerra, 1998; Cutzu & Tsotsos, 2003; Hopf et al., 2006; Hopf, Boehler, Schoenfeld, Heinze, & Tsotsos, 2010; Mounts, 2000; Muller, Mollenhauer, Rosler, & Kleinschmidt, 2005; Vanduffel, Tootell, & Orban, 2000). A typical receptive field may contain more than one stimulus or event, and for a typical task, only a subset may be relevant. If the relevant is considered 'the signal', then what remains is 'the noise'. Suppression of the noise improves the contrast or signal-to-noise ratio (SNR) leading to neural responses more closely representing the relevant stimuli. Subsequent modeling efforts have followed suit by incorporating parameters within modeling equations to express attentive gain changes in order to manipulate SNR (Boynton, 2005; Desimone & Duncan, 1995; Lee & Maunsell, 2009; Reynolds & Heeger, 2009).

The presence of distractors may decrease SNR, Some researchers already pointed out that increasing task difficulty would increase the allocation of attention (Boudreau, Williford, & Maunsell, 2006), and modify center-surround pattern of spatial attention (Chen et al., 2008). For auditory attention, Atiani et al. (2009) also found that in low SNR tasks but not high SNR tasks the far-from-target cells were suppressed. There is also physiological evidence that feature-based attention not only modulates response baseline and gain, but also alter neuronal tuning (David, Hayden, Mazer, & Gallant, 2008). However, we only found that the presence of distractors increased attention gain, but did not change the center-surround inhibition pattern. It could be that in our paradigm the presence or absence of distractors did not significantly change the SNR. Further studies are needed to clarify these questions.

Attentive spatial suppression has a spatial shape similar to a Difference of Gaussians profile.

This also was predicted in Tsotsos (1990) and supported by Slotnick et al. (2002), Müller et al. (2004), and Hopf et al. (2006). Perhaps of even greater interest, is the prediction, from the same paper, that surround suppression is due to top-down (recurrent) processes. McCarley et al. (2007), Boehler et al. (2009) both found evidence, psychophysical and neurphysiological, respectively. As several previous authors have also argued - Milner (1974), Fukushima (1986), Fuster (1990) - ST also argues for a top-down approach to attentional selection, and this now has experimental support. Here we further confirmed that attending to a particular feature would also result in a center-surround inhibition around that feature.

Of course, this is not the full breadth of attentional effects. For example, auditory attention seems to also exhibit some of the same phenomena. Researchers had found center-surround inhibition in semantic network: attending to a word may inhibit the retrieval of words with semantic similarity but facilitate the retrieval of the same word (M. C. Anderson, Bjork, & Bjork, 1994; M.C. Anderson, Green, & McCulloch, 2000; Barnhardt, Glisky, Polster, & Elam, 1996; Carr & Dagenbach, 1990). Recently researchers demonstrated that auditory attention showed a similar center-surround pattern as visual attention (Atiani, et al., 2009). Finally, Loach et al. (2008) examined whether or not the kind of attentional mechanism ST proposes applies throughout the cortex and not only for vision. If so, then similar suppression of competing actions should be observed and they show that an attentional mechanism inhibits competing motor programs that could elicit erroneous actions. They briefly presented pictures of door handles: a prime handle followed by a probe handle and manipulated the kind of grasping affordance each depicts using color and a texture and the orientation of the handle with respect to the subject's handedness. Texture is a tactile, and therefore action-relevant, dimension whereas color is not. It would activate a motor program for acting on the handle and color would not. In the first experiment, subjects were asked to respond to the texture and in the second, to the color. Participants made speeded key-press responses to the probe handle. Each responding hand was assigned a response key, so that it was either compatible or incompatible with the door handles, which faced to the right or left. We predicted that presentation of the prime handle for the texture task would elicit the generation of a motor program suitable for a reach of that orientation. Surround inhibition associated with this motor program should inhibit other motor programs coding for slightly dissimilar reaches. Thus, if the subsequently presented probe handle elicits a reach within that range, it would require the activation of a recently inhibited motor program. In contrast, the color task, not being a tactile one, would not show this suppression. Sure enough, suppressive surround effects due to attention were clearly observed, the first time they have been observed behaviorally in the motor domain. These suggest that ST may indeed describe a broader attentional mechanism applicable to any sensory or sensory-motor selection process.

Future experiments that investigate other feature domains, such as binocular disparity, are needed as well as an examination of how joint attention to combinations of features may interact. Attentional feature surround suppression is a powerful mechanism in the arsenal of attention that may participate in the dynamic tuning of the visual system to enable it to best respond to the input and task at hand (Tsotsos, 2011) within the constraints of its limited resources.

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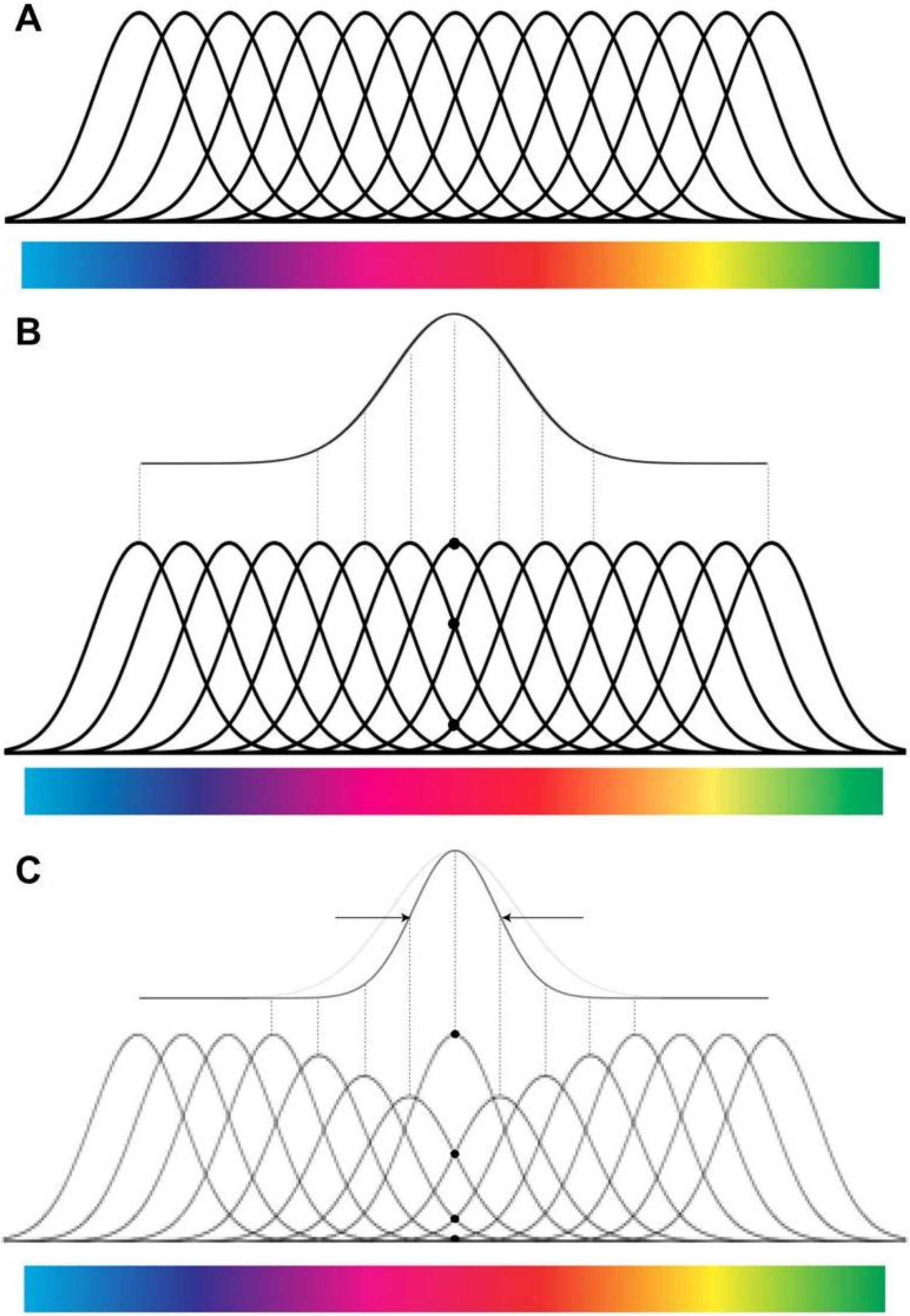
Figure Captions

Figure 1. A. Hypothetical tuning profiles for hue selective neurons across the color spectrum. B. The overall population response for a 'red' stimulus showing the typical peak at 'red'. C. The same profiles but with suppression around the attended hue of red and the resulting overall population response clearly showing a narrowing of tuning.

Figure 2. A. The striped disks used in experiment 1 & 2. The subjects were asked to indicate whether the stripes on the disk were straight (left) or jagged (right). B. The stimuli presentation sequence of experiment 1. C. The stimuli presentation sequence of experiment 2.

Figure 3. A. The subjects' average d′ under different probe conditions in experiment 1 & 2. The dot line represents the result of experiment 1 and the solid line experiment 2. The error bars represents one standard error. B. The ten individual subjects' sensitivity d′ under different probe conditions in experiment 1. Each line represents one subject. C. The nine individual subjects' sensitivity d′ under different probe conditions in experiment 2. Each line represents on subject.

Figure 4. A. The subjects' average d′ under different probe conditions in experiment 3. B. The ten individual subjects' sensitivity d′ under different color probe conditions in experiment 3. Each line represents on subject.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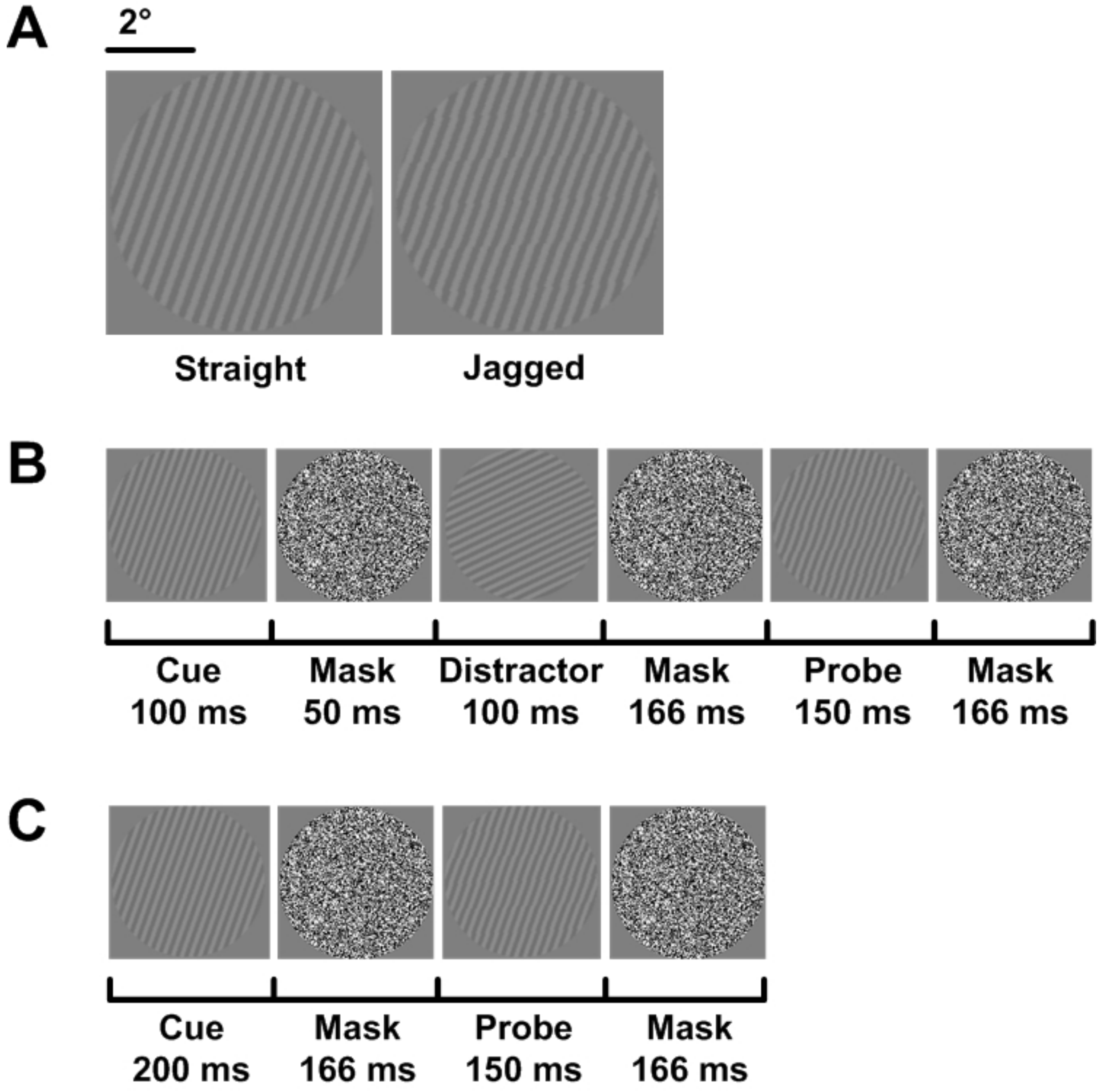
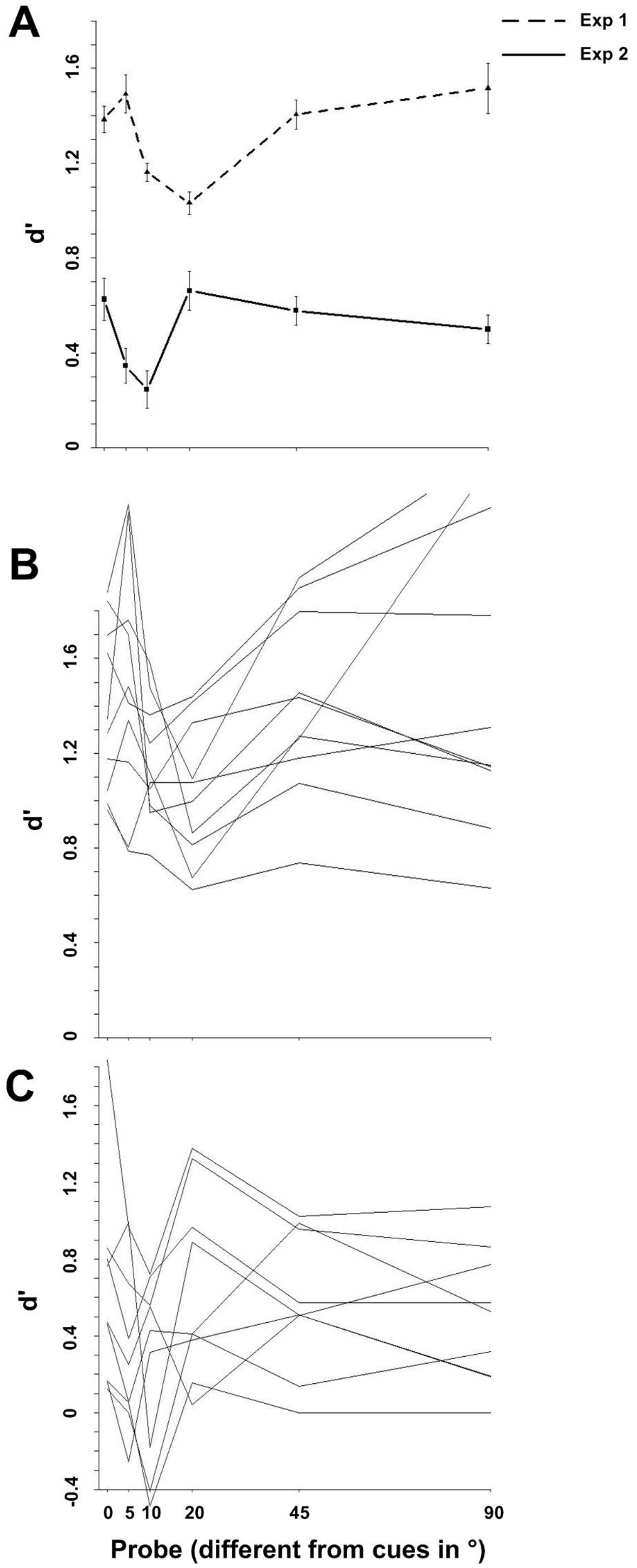
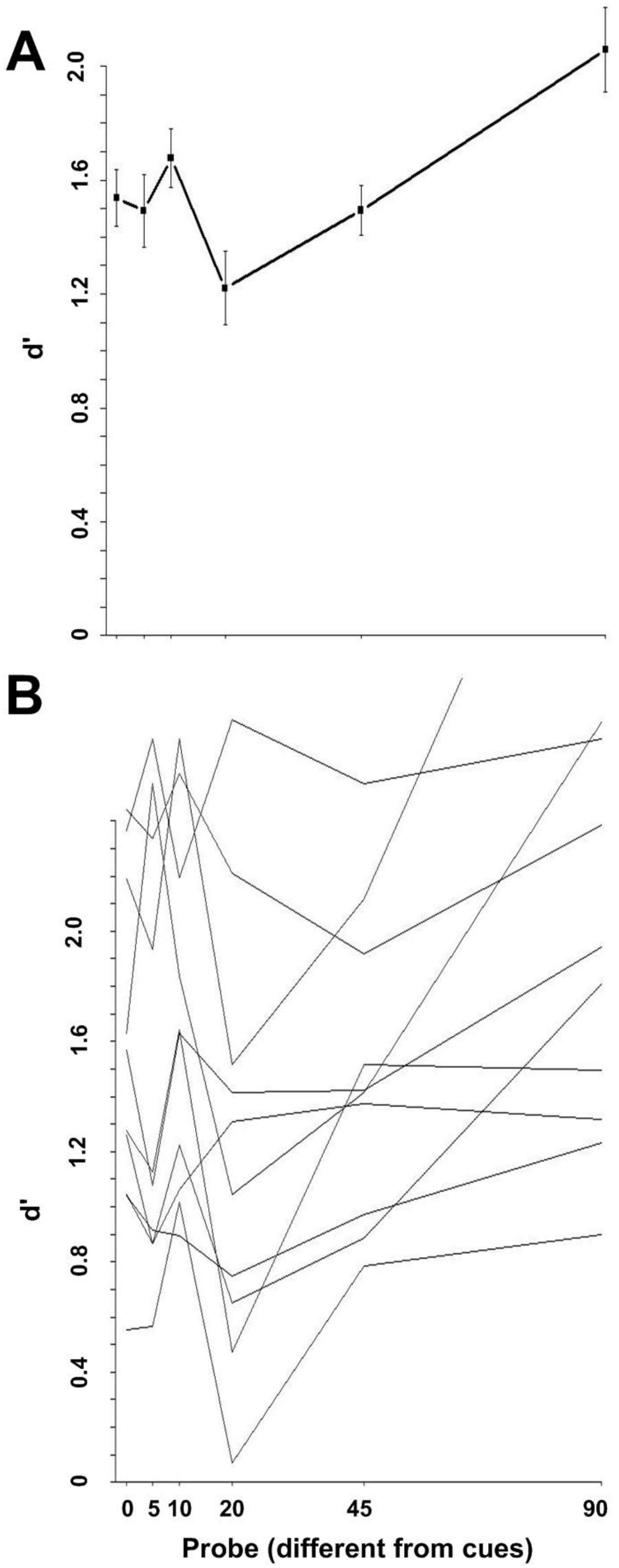
B
C


A
2°
Straight
Jagged
B
Cue 100 ms
Mask 50 ms
Distractor 100 ms
Mask 166 ms
Probe 150 ms
Mask 166 ms
C
Cue 200 ms
Mask 166 ms
Probe 150 ms
Mask 166 ms


A
B
C
Exp 1
Exp 2
d'
0
0.4
0.8
1.2
1.6
-0.4
0 5 10 20 45 90
Probe (different from cues in °)


A
2.0
1.6
1.2
0.8
0.4
0
d'
B
2.0
1.6
1.2
0.8
0.4
0
d'
0
5
10
20
45
90
Probe (different from cues)