Shape effects on reflexive spatial attention are driven by the dorsal stream ☆

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ARTICLE INFO

ABSTRACT

In a modified reflexive spatial attention paradigm, when the cue and the target are at the same spatial location, processing of the target is faster when the cue and the target have different shapes compared to same (shape effect). Recent physiological findings suggest distinct population level encoding of shape in ventral versus dorsal cortical visual streams in monkeys. In human observers, we tested whether the effect of shape on reflexive spatial attention could be attributed to ventral and/or dorsal stream encoding of shape. In the modified reflexive spatial attention paradigm, we varied the shapes of the cue and target. Based on data from monkey physiology (Lehky & Sereno, 2007), we selected four pairs of cue and target shapes. In some pairs, cue and target were similarly encoded (similar encoding distance) by a population of cells in the lateral intraparietal cortex, a dorsal stream area, but more dissimilarly encoded (having a greater encoding distance) by a population of cells in the anterior inferotemporal cortex (AIT), a ventral stream area. In other pairs, cue and target were similarly encoded in AIT and had greater dissimilarity in LIP encoding. We found that pairs of cue and target with greater dissimilarity in LIP encoding produced larger and more consistent shape effects up to a cue to target onset asynchrony (CTOA) of 450 ms. The shape effects for cue and target pairs with greater dissimilarity in AIT encoding were smaller and inconsistent, suggesting that shape effects in reflexive spatial attention are largely driven by the dorsal stream.

1. Introduction

Although the human brain is made up of billions of neurons, it is unable to thoroughly deal with even a small fraction of the information that is received. The process of attention works to filter out and select the most relevant information in an effort to use the brain's limited resources in the most efficient manner. Attention can be willful (voluntary) or more passive (reflexive) (Jonides & Irwin, 1981; Moore, 2006; Nakayama & Mackeben, 1989; Sereno & Amador, 2006). Previously we have proposed a neurophysiologically based model of reflexive spatial attention and tested a key prediction of the model that the shape of the cue and the target should modulate reflexive spatial attention (Patel, Peng, & Sereno, 2010; Sereno et al., 2010). This study is focused on determining the neuroanatomical locus of those shape-dependent modulations in reflexive attention.

In a typical reflexive spatial attention paradigm, the observer performs a spatial localization task. In such a task, the subject is presented with a behaviorally irrelevant cue followed by a target.

The spatial locations of the cue and the target are randomly varied. In some trials, the cue will be in the same location as the target (cued trials), and in other trials the cue and the target will be in different spatial locations (uncued trials). The time delay between the onset of the cue and the onset of the target, or cue to target onset asynchrony (CTOA), is varied randomly from trial to trial. Depending on the CTOA, the response to the target on cued trials can be facilitated or inhibited compared to uncued trials, as indicated by faster or slower response times for reporting the location of the target. Typically, a facilitation in the response for cued compared to uncued trials occurs with shorter CTOAs, while inhibition is seen with longer CTOAs (Posner & Cohen, 1984). The inhibition in cued compared to uncued trials is termed inhibition of return. These reflexive spatial attention effects have been shown using tasks with manual responses as well as with eye movement responses (Briand, Larrison, & Sereno, 2000; Taylor & Klein, 2000).

Recent work shows that the shapes of the cue and target influence the time course and magnitude of these spatial attentional effects (Patel, Peng, & Sereno, 2010). They found that manual response times for CTOAs from 116 to 400 ms were longer for cued trials in which the cue and the target were the same shapes compared to when they were different (i.e., shape effect = Response time$_{different\ shape}$ − Response time$_{same\ shape}$). For uncued trials, where the cue and target appeared in different locations, a shape effect was not found.

1.1. Neural mechanism of spatial cueing effects

In an effort to understand the neural activity underlying behavioral spatial cueing effects, Dorris et al. (2002), used a task requiring eye movement responses and recorded from the superior colliculus (SC). They found that slower saccadic response times during IOR did correlate with a weakened neural response in SC to target presentation. Nevertheless, Dorris et al. (2002) concluded that SC was not the site of inhibition underlying IOR because (1) neurons in the superior colliculus (SC) were *more active* after the cue and before the target presentation at time intervals that would normally lead to IOR; and (2) if these SC neurons were stimulated during this same time interval, this elevation in activity also resulted in faster saccade latencies (not slower, as would be expected by the slower latencies during IOR. Hence, they suggested that the site of inhibition is likely upstream to SC in parietal areas associated with the dorsal cortical visual pathway (Dorris et al., 2002).

Sereno and colleagues (Patel, Peng, & Sereno, 2010; Sereno et al., 2010) have suggested that despite the elevated neural activity after cue presentation, the reduced neural response to a repeated stimulus (as was the case for the targets in Dorris et al. (2002) could be a key mechanism underlying IOR and reflexive spatial attention. That is, one possible neuronal mechanism for the increase (i.e., inhibition) of response times could be repetition suppression, a phenomenon that has been reported for shape stimuli in both ventral and dorsal cortical visual processing streams (Lehky & Sereno, 2007) as well as for luminance targets in the superior colliculus (Fecteau, Bell, & Munoz, 2004). During repetition suppression, a neuron's response to a stimulus is reduced upon subsequent presentations of the same stimulus (Baylis & Rolls, 1987; Brown & Bashir, 2002; Brown, Wilson, & Riches, 1987; Fahy, Riches, & Brown, 1993; Gross, Bender, & Gerstein, 1979; Miller, Gochin, & Gross, 1991; Miller, Li, & Desimone, 1993; Rolls et al., 1989; Sobotka & Ringo, 1993; Xiang & Brown, 1998).

Patel, Peng, & Sereno (2010; see also Sereno et al., 2010) constructed a neurophysiologically plausible model of reflexive spatial attention that showed both facilitation at short CTOAs and IOR at long CTOAs, as well as a shape effect at CTOAs up to 600 ms (i.e., slowing of response times on cued trials when the cue and target were the same shape). Repetition suppression was not only a main but critical property of this model. Thus, we suggested that repetition suppression may be a possible neural mechanism underlying the behavioral effects, including both the spatial cueing effects and shape effects, in a reflexive spatial attention paradigm (Patel, Peng, & Sereno, 2010; Sereno et al., 2010). Furthermore, such a widely documented mechanism suggests that reflexive spatial attentional effects are a distributed property of the brain and that these spatial and shape effects may manifest in different forms, depending on the different properties and selectivities of different brain regions (Sereno et al., 2010). We attempt here to establish the anatomical locus of this particular shape effect in reflexive spatial attention in an effort to gain a better understanding of the functional role of shape selective cells from distinct cortical areas (e.g. LIP or AIT) in spatial attention.

1.2. Shape processing in dorsal and ventral streams

Although LIP and the dorsal stream are typically associated with spatial processing and anterior inferotemporal cortex (AIT) and the ventral stream with shape processing and object recognition, several groups have now reported shape selective cells in LIP (Janssen et al., 2008; Sereno & Amador, 2006; Sereno & Maunsell, 1998) and other dorsal stream areas (Murata et al., 2000; Peng et al., 2008). In a direct comparison of shape encoding in ventral (AIT) and dorsal cortical streams, Lehky and Sereno (2007) showed that while cells in both areas encode for shape, populations of shape selective cells in LIP exhibit a distinct and unique encoding of shapes when compared to populations of AIT cells.

The purpose of parallel shape encoding in ventral and dorsal streams remains unclear. As discussed by Peng et al. (2008), shape could be encoded differently in the dorsal and ventral stream to accomplish different goals. Dorsal stream encoding of shape could be more useful for tasks that require guiding motor behaviors, such as needed in a reflexive spatial attention task with localization response. On the other hand, ventral stream shape encoding may be better suited for tasks involving object recognition (Peng et al., 2008), such as required in a discrimination task. Thus, one might expect in a reflexive attention task with localization response that shape effects would be dependent on dorsal stream shape encoding. To the best of our knowledge, this would be the first demonstration of a functional role for these dorsal stream shape responses. That is, it would show that shape selective neurons in the dorsal stream are playing a critical role in reflexive spatial attention.

1.3. Similarities between human and monkey visual processing

Differences in dorsal and ventral stream encoding of shape have only recently been documented, and only in monkey (Lehky & Sereno, 2007; Szczepanski, Konen, & Kastner, 2010). Using these differences to establish the anatomical locus of shape effects in humans will be successful only if there is similarity between these species in visual processing, and shape encoding, in particular. Much early work, primarily based on physiological recordings, found a relatively continuous representation of shape with little evidence for regions specialized for different individual classes of objects in monkey inferior temporal (IT) cortex, with the exception of faces (Tanaka, 1996). In contrast, based primarily on fMRI, human IT was thought to be more modular with regions specialized for faces or buildings (Aguirre, Zarahn, & D'Esposito, 1998; Kanwisher, McDermott, & Chun, 1997; Tsao et al., 2006). Recently, in more direct comparisons, various findings suggest instead similarity in visual representations between humans and monkeys, even for categorical and conceptual abilities (Fize, Cauchoix, & Fabre-Thorpe, 2011; Kriegeskorte et al., 2008; Sigala, Gabbiani, & Logothetis, 2002). Specifically, Kriegeskorte et al., 2008, using representational similarity analysis (RSA), found that monkey and human IT emphasize very similar distinctions among objects and that both species may host a common code, which combines both a categorical and continuous representation of objects. RSA and other multidimensional scaling techniques allow for quantitative comparison of different representations and have been successfully implemented to compare representations across brain regions, different species, and different tasks (Kriegeskorte et al., 2008; Lehky & Sereno, 2007; Sereno & Lehky, 2011). Although recent work suggests a common representation of shape across species in IT, we are aware of no studies that have compared shape encoding in dorsal stream across species. Even though shape encoding in LIP has not been specifically compared in humans and monkeys, areas within the human intraparietal sulcus have been suggested to be homologs to monkey LIP (Culham & Kanwisher, 2001; Sereno, Pitzalis, & Martinez, 2001) see also (Orban et al., 2006; Szczepanski, Konen, & Kastner, 2010).

1.4. Present study

If shape encoding in dorsal and ventral streams in humans is similar to that in monkeys then the reported differences in shape encoding between ventral and dorsal streams (Lehky & Sereno, 2007) can be used to tease apart the neuronal basis of the shape effect observed in human spatial attention (Patel, Peng, & Sereno,

2010). That is, using the response distances between pairs of shapes (a distance metric based on populations of cells in LIP and AIT of monkeys; Lehky & Sereno, 2007), we formed a set of four pairs of shapes. Shapes with a smaller *response distance* indicated that the population of neurons fired similarly to these shapes. Lehky and Sereno (2007) used a correlation-based measure of distance ($d = 1 - r$), thus a smaller distance between a pair of shapes indicated a higher correlation in the population responses to these shapes. In this set, one pair of shapes had the largest response distance (greatest dissimilarity) between the two shapes in AIT (AIT$_{max-dissimilar}$ pair). The remaining three pairs had nearly equal and smaller response distances in populations of AIT cells than the AIT$_{max-dissimilar}$ pair. Additionally, in this same set of four pairs of shapes, one pair (different from the AIT$_{max-dissimilar}$ pair) had the largest response distance in LIP (LIP$_{max-dissimilar}$ pair). The remaining three pairs had nearly equal and smaller response distances in populations of LIP cells than the LIP$_{max-dissimilar}$ pair.

For each shape pair in the set, spatial and shape cueing effects were determined using the modified reflexive spatial attention paradigm (Patel, Peng, & Sereno, 2010). Recall that the shape effect is dependent on the dissimilarity of the cue and target (i.e., shape effect = RT$_{different-shape}$ − RT$_{same-shape}$). In the different shape trials, the shape of the cue and the target are different, but if the shape response distance is smaller, the difference in RT between different- and same-shape trials (i.e. shape effect) will be smaller (or even nonexistent). Thus, more dissimilarly encoded shape pairs will have larger shape effects than less dissimilarly encoded shape pairs. If dorsal stream were primarily responsible for the shape effect, the shape effect would be maximal for the LIP$_{max-dissimilar}$ pair compared to the control pairs (described later in Methods section). If ventral stream were primarily responsible for the shape effect, this difference would be maximal for the AIT$_{max-dissimilar}$ pair compared to the control pairs. If both streams played a role, shape effects would be present for both the LIP$_{max-dissimilar}$ and AIT$_{max-dissimilar}$ pairs. If our shapes were too similar or the differences in physiological response too small to engender behavioral differences, we might not see any significant differences in shape effects between shape pairs and we would not be able to determine if the shape effects were driven primarily by dorsal or ventral stream.

Thus, in this study, we specifically sought to determine if there was a relationship between the size of the shape effect, as measured behaviorally, and shape response distances previously reported for populations of AIT and LIP neurons in monkeys. We interpreted the relative contributions of ventral (AIT) and dorsal brain areas by measuring the magnitude of shape effects under different conditions and testing whether they were more consistent with a ventral and/or dorsal encoding of shape.

2. Methods

2.1. Subjects

Six subjects (five male, one female, age range 22–24), including five naïve and one author, participated in all the experiments. Informed consent was obtained from each observer and the study was approved by the Committee for the Protection of Human Subjects at our institution in accordance with the Declaration of Helsinki. After the experiments were completed, one of the subjects was found to have fasted for several days during the experiments and his data were excluded from the analyses.

2.2. Apparatus

Stimuli were presented using a ViewSonic computer monitor (15 in. LCD, 4 ms response-time, 1280 × 1024, 60 Hz) at a distance


Shape Pairs	Pair #	AIT	LIP
●◆	1	.45	.03
■▯	2	.31	.17
✚▦	3	.27	.03
◣◥	4	.29	.03

Fig. 1. Shape pairs (column 1) and their associated neural population response distances from Lehky and Sereno (2007). The population response distance between each shape pair is shown for populations of shape selective cells in AIT (third column) and LIP (fourth column). A larger response distance value indicates greater distinctiveness (dissimilarity) in neuronal responses across a sample population of shape selective cells. The population response distances with highest value (highest dissimilarity) for each area are highlighted in grey (i.e., AIT$_{max-dissimilar}$ pair = 0.45; and LIP$_{max-dissimilar}$ pair = 0.17). The remaining three pairs in each area had nearly equal distances in AIT and LIP (AIT$_{mean}$ = 0.29; and LIP$_{mean}$ = .03). Shape Pairs 3 and 4 were in combination treated as a control pair for both AIT$_{max-dissimilar}$ and LIP$_{max-dissimilar}$ pairs.

of 62.5 cm, using a chin-rest. Each pixel was 1.4 arc-min. Experiments were performed in a quiet, darkened room. A custom built box with two push buttons (for left and right index fingers) was directly connected to the computer via an ITC-18 Instrutech Corporation data acquisition interface, and had a temporal resolution of 100 microseconds for response time (RT) data. Analog signals from the push buttons were digitized to compute the RTs. Stimuli were presented and data were collected and analyzed using custom software developed using the Psychophysics Toolbox (Brainard, 1997) for Matlab.

2.3. Stimuli

The fixation stimulus was a small white square (8 × 8 pixels, 0.2 × 0.2°, 187 cd/m^2) that was presented at the center of a dark screen. Based on physiological data from Lehky and Sereno (2007), we selected four pairs of shapes for the cue and the target (Fig. 1). Each cue and target stimuli were of equal luminance
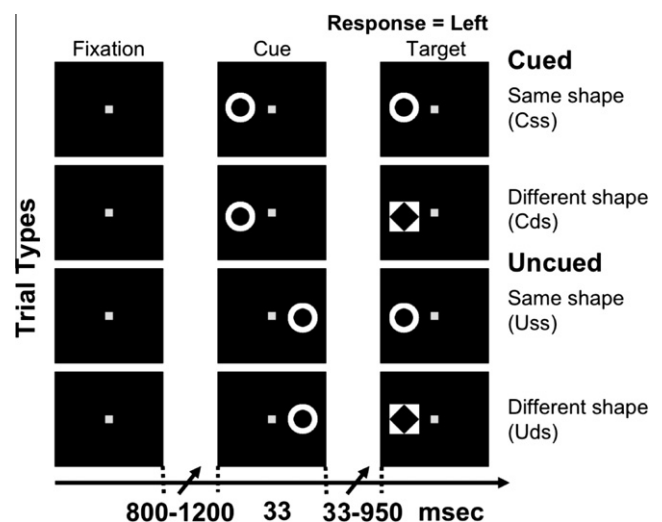
Fig. 2. Modified reflexive attention paradigm. The four different trial types are shown: cued same shape (Css), cued different shape (Cds), uncued same shape (Uss), and uncued different shape (Uds). Time is represented by the horizontal arrow at the bottom. The left column represents the fixation period (800–1200 ms), which is followed by a cue (33 ms) either on the left or right of the fixation point. After a random delay (33–950 ms), the target appeared and remained present until the subject responded (correct response for all four examples is to saccade to the left).

(187 cd/m^2) and constructed in a square of 64×64 pixels $(1.5 \times 1.5°)$. For all the shapes, the number of bright pixels was similar.

2.4. Procedure

Response time data was collected in six sessions for each observer. Every session consisted of 16 runs with four runs of each of the four shape pairs. In each run, the shape pair remained fixed. From session to session, the order of the runs was counterbalanced to vary the order in which shape pairs were presented. Observers initiated a trial by pressing and holding both push buttons. After an initial variable fixation period (800–1200 ms) a cue was displayed for 33 ms. The target was then presented after a randomly selected delay from a set of six possible CTOAs: 66, 99, 183, 283, 483 and 983 ms. The same set of six CTOAs was used for all runs. The cue and the target could appear in either the same or different location (randomly offset horizontally at 5° eccentricity on either side of fixation). The shapes of the cue and the target were randomly the same or different in each trial, but balanced equally (Fig. 2 shows one example pair, with response left). Each run with a particular shape pair consisted of 96 trials (2 locations $[-5$ and $5°] \times 2$ cue shapes $\times 2$ target shapes $\times 2$ spatial cueing conditions [cued or same-side versus uncued or opposite-sides] $\times 6$ CTOAs). Therefore, data was collected on 2304 trials (6 sessions $\times 4$ runs $\times 96$ trials) for each observer on each shape pair and 9216 total trials for each observer (6 sessions $\times 4$ runs $\times 4$ shape pairs $\times 96$ trials). Observers were asked to fixate on the fixation stimulus, ignore the cue stimulus, and respond as quickly as possible to the target stimulus by releasing the button on the side corresponding to the location of the target. To avoid engendering voluntary effects, subjects were explicitly told that the cue's shape and location would not predict the shape and location of the target. Thus in our design spatial or shape expectations for the target (either planned or unplanned) were not induced. The target remained on the screen until the observer responded. The inter-trial interval was 500 ms.

2.5. Data analysis

For each shape pair, RT data were sorted into four trial types based on the shape and location of the cue and the target. The trial types were: Cued same-shape (Css), Cued different-shape (Cds), Uncued same-shape (Uss), Uncued different-shape (Uds) (see Fig. 2). Spatial cueing and shape effects were computed as described in Table 1.

Trials with errors (3.9%) were eliminated and not further analyzed. For each observer, shape pair, trial type and CTOA, the remaining data were iteratively trimmed until all RTs were within 2.5 standard deviation of the mean RT. The iterative trimming procedure removed 9.0% of all error-free trials (note that the first iteration only removed 3% of trials).

RT data were analyzed using mixed effects models with subject as a random effect. All analysis models used the auto-regressive covariance structure. First, mixed model analyses were conducted separately for each CTOA (*first mixed model analyses*). In each analysis, the fixed effects were trial type (four levels: Css, Cds, Uss, Uds), shape pair {three levels: shape pair $\text{AIT}_{\text{max-dissimilar}}$ (Shape Pair 1), shape pair $\text{LIP}_{\text{max-dissimilar}}$ (Shape Pair 2), and control pair

Table 1
Computation of cueing effects.

Cueing effect	Equation
Cued shape effect	Cds–Css
Uncued shape effect	Uds–Uss
Different shape spatial cueing effect (standard)	Uds–Cds
Same shape spatial cueing effect	Uss–Css
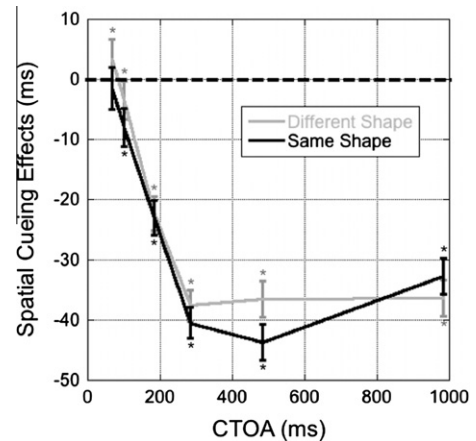
Fig. 3. Spatial cueing effects averaged across all the observers and shape pairs as a function of CTOA for different and same shape trials. Positive values on the *y*-axis are considered facilitatory spatial cueing effects while negative values are inhibitory spatial cueing effects. The error bars represent ±2 standard errors of the mean. An asterisk represents a significant difference from zero.

(Shape Pairs 3 and 4 were treated as one control pair)}, and their interaction. If a statistically significant fixed effect was found, the post hoc contrasts were constructed to investigate the spatial cueing effects (Fig. 3) and shape effects (Fig. 4) averaged across all shape pairs for the corresponding CTOA.

Next, mixed model analyses were conducted separately for each CTOA and each shape pair (*second mixed model analyses*). In each analysis, the fixed effect was trial type (four levels as described above). If a statistically significant effect was found, the post hoc contrasts were constructed to investigate the shape effects for the corresponding shape pair and CTOA (see Fig. 5).

Finally, mixed model analyses were conducted separately for each shape pair (*third mixed model analyses*). In these analyses, in contrast to the previous two analyses where the dependent variable was RT averaged only across trials, the dependent variable was the RT averaged across all the trials of the first five CTOAs (CTOAs where shape effects might be observed). This averaging was done to account for the substantial variability across CTOAs. In the third mixed model analyses, the fixed effect was trial type (four levels, as described above). If a statistically significant effect was found, the post hoc contrasts were constructed to investigate the shape effects for the corresponding shape pair (see Fig. 6). Further, contrasts were also made between the shape effects (averaged across the first five CTOAs) of the max-dissimilar shape pairs and the control shape pair (see Fig. 6). A biostatistician conducted the statistical analyses using SAS 9.2 for Windows (Cary, NC). A *p*-value $\leqslant 0.05$ was considered as statistically significant.

3. Results

3.1. Effects of trial type, shape pair and their interaction on RT

Table 2 shows the summary of the first mixed model analyses. The fixed effect of trial type was significant for CTOAs of 99, 183, 283, 483, and 983 ms. Post hoc contrasts were constructed to further investigate the spatial cueing and shape effects and are discussed below. Shape pair was a significant fixed effect for all the CTOAs. The interaction of trial type and shape pair was found to be significant only at the CTOA of 99 ms.

3.1.1. Spatial cueing effects averaged across shape pairs

Spatial cueing effects were examined using contrasts from the first mixed model analyses. Fig. 3 shows the spatial cueing effects for different- and same-shape trials averaged across all the observ-
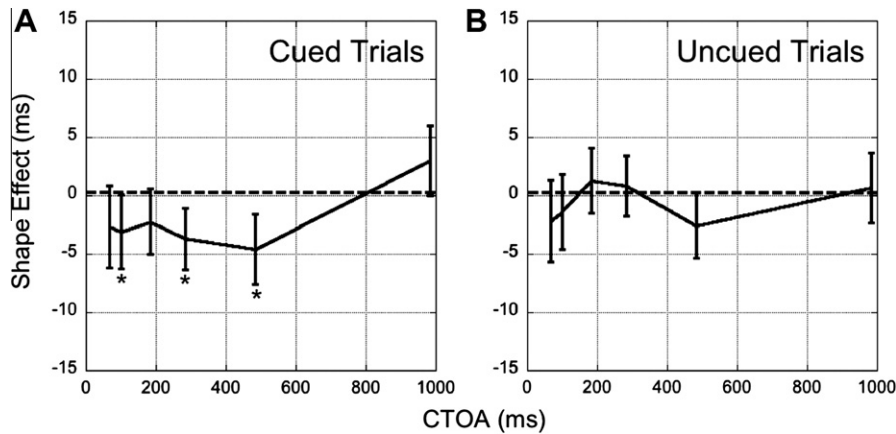
Fig. 4. Shape effects averaged across all the observers and shape pairs as a function of CTOA for cued (panel A) and uncued (panel B) trials. Positive values on the *y*-axis are considered facilitatory shape effects while negative values are inhibitory shape effects. The error bars represent ±2 standard errors of the mean. An asterisk represents a significant difference from zero. Note expanded *y*-axis scale compared to spatial cueing effects in Fig. 3.
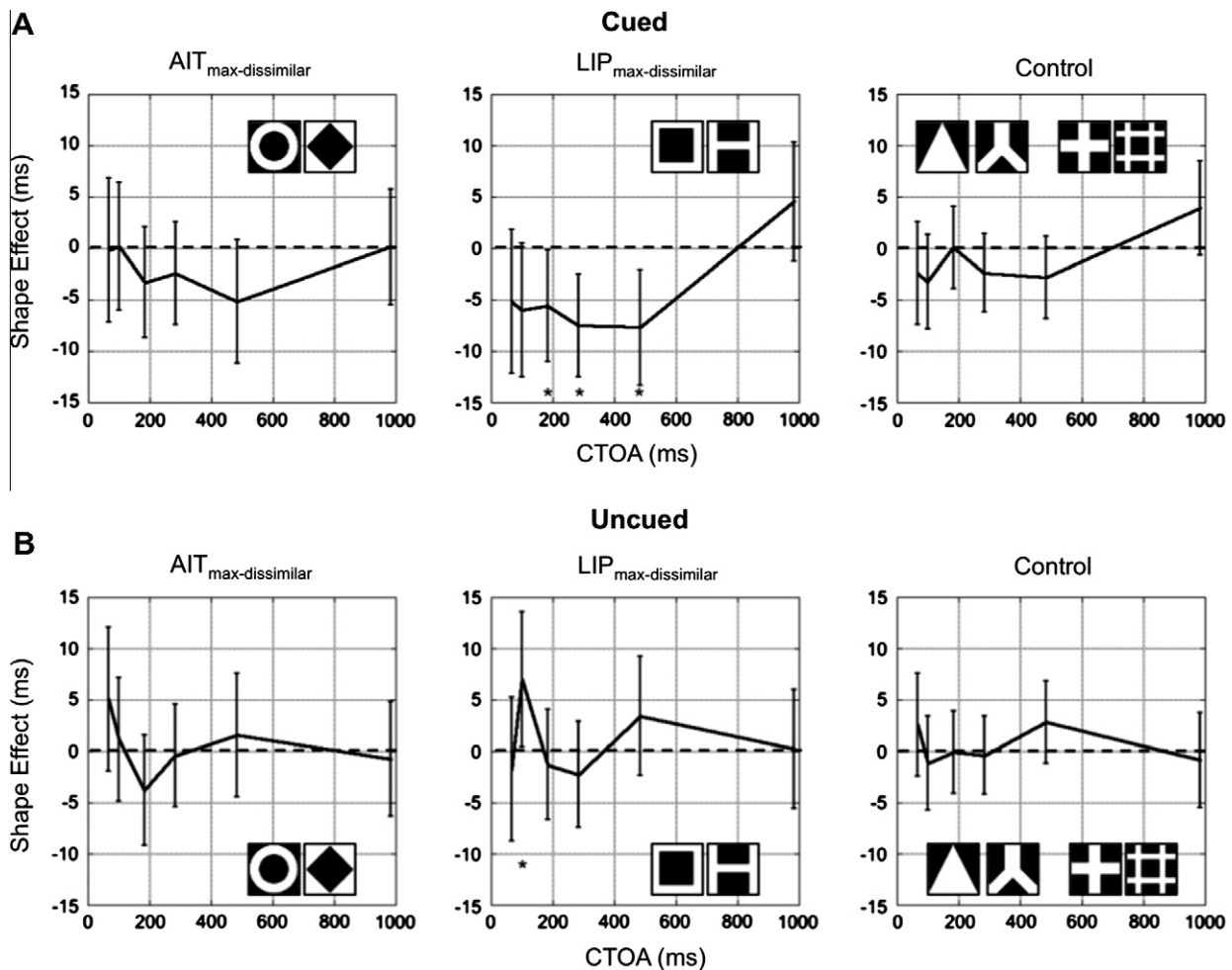
Fig. 5. Shape effects averaged across all the observers in cued (panel A) and uncued (panel B) trials for $AIT_{max-dissimilar}$, $LIP_{max-dissimilar}$ and control shape pairs as a function of CTOA. All other conventions are the same as in Fig. 4.

ers and shape pairs (gray and black line respectively; for mean RT values see Table 3). A significant ($p < 0.05$) inhibitory spatial cueing effect, or IOR, was found for CTOAs of 99, 183, 283, 483, and 983 ms for both the different (gray line, Fig. 3) and same shape trials (black line, Fig. 3).

The relatively small facilitation and magnitude of the shape effect for these stimulus conditions is most likely due to the relative

similarity of the shapes in all our cue and target pairs. In particular, three of the four target pairs in the "different shape" condition being averaged together here were selected to minimize physiologically-based dissimilarity. We have previously demonstrated in both behavior and modeling that shape similarity of the cue and target reduces the early spatial facilitation (Patel, Peng, & Sereno, 2010). Despite the similarity of our cues and targets, we
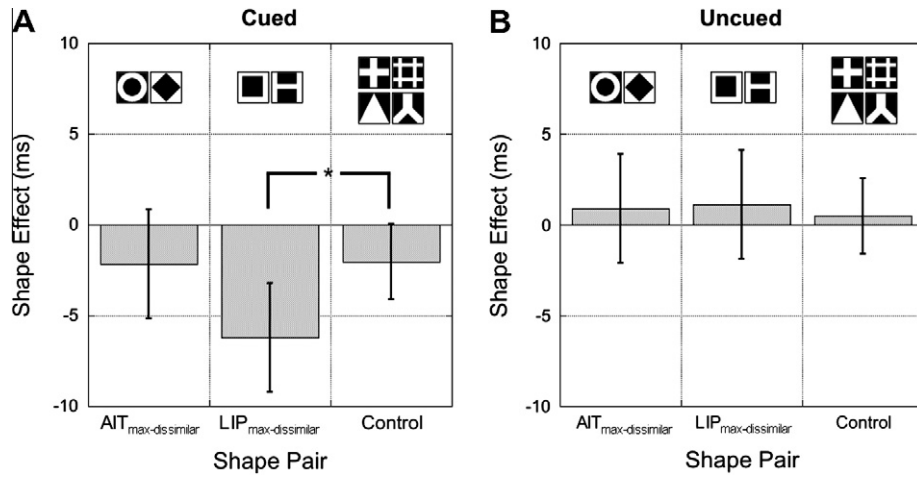
Fig. 6. Shape effects in cued (panel A) and uncued (panel B) trials for $AIT_{max-dissimilar}$, $LIP_{max-dissimilar}$ and control shape pairs averaged across the first five CTOAs. Asterisk denotes significant difference between shape effects for $LIP_{max-dissimilar}$ and control shape pairs.

Table 2
Summary of mixed model analysis with effects of trial type, shape pair, and their interaction on RT.

CTOA (ms)	Trial type				Shape pair				Trial type × Shape pair			
	Num. DF	Den. DF	F value	p Value	Num. DF	Den. DF	F value	p Value	Num. DF	Den. DF	F value	p Value
66	3	6610	1.54	0.20	2	6610	4.17	**0.02**	6	6610	1.65	0.13
99	3	6610	7.60	**<0.001**	2	6610	3.19	**0.04**	6	6610	2.44	**0.02**
183	3	6610	161.01	**<0.001**	2	6610	3.81	**0.02**	6	6610	0.97	0.44
283	3	6610	541.08	**<0.001**	2	6610	5.25	**0.005**	6	6610	0.91	0.49
483	3	6610	451.92	**<0.001**	2	6610	6.72	**0.001**	6	6610	0.53	0.79
983	3	6610	322.89	**<0.001**	2	6610	9.21	**<0.001**	6	6610	1.49	0.18

Significant p values are shown in bold. Num. DF refers to the numerator degrees of freedom and Den. DF refers to the denominator degrees of freedom.

Table 3
Mean RT values for each trial type at each CTOA.

CTOA (ms)	Cued (ms)				Uncued (ms)			
	Same shape		Different shape		Same shape		Different shape	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
66	323.0	1.4	320.5	1.3	321.3	1.3	323.3	1.4
99	310.9	1.3	307.9	1.4	303.2	1.3	304.5	1.4
183	297.4	1.3	294.9	1.4	274.1	1.3	273.0	1.4
283	304.9	1.3	298.5	1.4	257.6	1.4	256.9	1.4
483	309.6	1.3	299.7	1.4	266.0	1.4	269.0	1.4
983	295.8	1.3	303.7	1.3	263.6	1.3	262.8	1.4

still see an additional downward shift in the spatial cueing effects for same shape trial types versus different-shape trial types at CTOAs less than 600 ms (Fig. 3, black line below gray line at short CTOAs). Thus, spatial cueing effects for both different and same shape trials were qualitatively similar to previous findings (Patel, Peng, & Sereno, 2010).

3.1.2. Shape effects averaged across shape pairs
Shape effects were also examined using contrasts from the first mixed model analyses. The shape effects on reflexive spatial attention for cued and uncued trials averaged across all the observers and shape pairs are shown in Figs. 4A and B, respectively (specific values of mean RTs are in Table 3). The shape effects for cued trials

Table 4
Summary of mixed model analysis for effect of trial type for each shape pair at each CTOA.

CTOA (ms)	$AIT_{max-dissimilar}$				$LIP_{max-dissimilar}$				Control			
	Num. DF	Den. DF	F value	p Value	Num. DF	Den. DF	F value	p Value	Num. DF	Den. DF	F value	p Value
66	3	1634	3.15	**0.02**	3	1649	0.88	0.45	3	3321	0.80	0.50
99	3	1635	0.05	0.98	3	1637	6.24	**<0.001**	3	3330	7.97	**<0.001**
183	3	1614	59.04	**<0.001**	3	1644	42.80	**<0.001**	3	3326	78.14	**<0.001**
283	3	1633	185.30	**<0.001**	3	1627	160.39	**<0.001**	3	3335	256.11	**<0.001**
483	3	1623	115.39	**<0.001**	3	1624	146.62	**<0.001**	3	3278	239.75	**<0.001**
983	3	1656	98.00	**<0.001**	3	1655	122.55	**<0.001**	3	3416	140.94	**<0.001**

Significant p values are shown in bold. Num. DF refers to the numerator degrees of freedom and Den. DF refers to the denominator degrees of freedom.

Table 5
Mean RT for each shape pair at each trial type and CTOA.

CTOA (ms)	AIT$_{max-dissimilar}$				LIP$_{max-dissimilar}$				Control			
	Same shape		Different shape		Same shape		Different shape		Same shape		Different shape	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Cued (ms)												
66	320.3	2.7	321.7	2.7	321.4	2.7	316.4	2.7	325.1	1.9	322.0	1.9
99	305.0	2.7	305.8	2.7	310.7	2.7	302.9	2.7	313.9	1.9	311.3	1.9
183	299.5	2.7	296.2	2.8	294.7	2.7	289.8	2.7	297.6	1.9	296.7	1.9
283	298.8	2.7	296.5	2.7	297.2	2.7	289.3	2.7	299.0	1.9	295.7	1.9
483	312.1	2.7	307.0	2.7	308.4	2.7	301.1	2.7	309.0	1.9	305.8	1.9
983	295.1	2.7	296.6	2.7	293.0	2.7	299.4	2.6	297.6	1.9	301.2	1.9
Uncued (ms)												
66	324.3	2.7	330.3	2.7	318.3	2.7	315.9	2.7	321.3	1.9	323.5	1.9
99	305.7	2.7	305.9	2.7	295.8	2.7	303.7	2.7	305.4	1.9	304.1	1.9
183	273.7	2.7	270.7	2.8	271.3	2.7	269.6	2.7	275.6	1.9	275.8	1.9
283	256.5	2.7	255.8	2.7	254.1	2.7	251.9	2.7	259.8	1.9	259.8	1.9
483	270.0	2.7	270.9	2.7	260.2	2.7	264.5	2.7	266.9	1.9	270.1	1.9
983	262.2	2.7	261.8	2.7	256.5	2.7	256.5	2.7	267.7	1.9	266.4	1.9

showed significant ($p < 0.05$) inhibitory shape cueing effects at CTOAs of 99 ($t = -2.02$, $p < .05$), 283 ($t = -2.97$, $p < .01$), and 483 ($t = -3.35$, $p < .01$) ms (Fig. 4A). As shown before (Patel, Peng, & Sereno, 2010), uncued trials did not produce a significant shape effect (Fig. 4B).

3.1.3. Shape effects for each shape pair

Table 4 shows the summary of the second mixed model analyses. The fixed effect of trial type was significant for CTOAs of 99, 183, 283, 483, and 983 ms. Post hoc contrasts were constructed to further investigate the shape effects and are discussed below.

Shape effects for each shape pair are shown in Fig. 5A (specific values of RTs for each shape pair are in Table 5). In cued trials, the shape effects for shape pair AIT$_{max-dissimilar}$ (Fig. 5A, left panel) were not significant for any CTOA. The inhibitory shape effects in cued trials for shape pair LIP$_{max-dissimilar}$ (Fig. 5A, middle panel) were significant ($p < 0.05$) at CTOAs of 183 ($t = -2.02$, $p < .05$), 283 ($t = -2.89$, $p < .01$), and 483 ($t = -2.71$, $p < .01$) ms. The control shape pair showed no significant shape effects in cued trials (Fig. 5A, right panel).

The neurophysiologically based model of reflexive spatial attention predicts an absence of shape effect in uncued trials (Patel, Peng, & Sereno, 2010; Sereno et al., 2010). This prediction was validated in a previous study (Patel, Peng, & Sereno, 2010) and was also examined for each shape pair in this study. Shape effects for each shape pair in uncued trials is shown in Fig. 5B (specific RTs for each shape pair are in Table 5). Except for one shape pair at one CTOA (shape pair LIP$_{max-dissimilar}$, CTOA of 99 ms, showing facilitation instead of inhibition), shape effects were absent in uncued trials.

3.1.4. Shape effects averaged across the first five CTOAs

Table 6 shows the summary of the third mixed model analyses. Each shape pair had a significant fixed effect of trial type. For each shape pair, shape effects were examined using contrasts and are described below.

Fig. 6 shows the shape effects averaged across the first five CTOAs for each shape pair (specific values of RTs averaged across the first five CTOAs are in Table 7). Shape pair LIP$_{max-dissimilar}$ had a significant ($t = -4.23$, $p < 0.001$) inhibitory shape effect in cued trials. The control shape pair also had a significant ($t = -1.95$, $p = 0.05$) shape effect in cued trials. All other shape effects were non-significant. Finally, the shape effects of the AIT$_{max-dissimilar}$ and LIP$_{max-dissimilar}$ were compared to the shape effect of the control pair. In cued trials, the inhibitory shape effect for shape pair

Table 6
Summary of mixed model analysis for mean RT of first five CTOAs for each shape pair.

Shape pair	Num. DF	Den. DF	F value	p Value
AIT$_{max-dissimilar}$	3	8171	119.2	<0.001
LIP$_{max-dissimilar}$	3	8213	157.7	<0.001
Control	3	17,000	276.6	<0.001

Num. DF refers to the numerator degrees of freedom and Den. DF refers to the denominator degrees of freedom.

LIP$_{max-dissimilar}$ was significantly larger than that for the control shape pair ($t = 1.96$, $p = 0.05$) but the shape effect for shape pair AIT$_{max-dissimilar}$ was not different from that for the control shape pair ($t = -0.04$, $p = 0.97$).

4. Discussion

Consistent with previous findings of Patel, Peng, and Sereno (2010), we found inhibitory shape effects in cued trials for CTOAs up to 483 ms (Figs. 4 and 5). The magnitude of shape effects depended on the shape pair (Figs. 5 and 6) with the most consistent shape effects obtained with shape pair LIP$_{max-dissimilar}$ (Figs. 5A and 6A). These results suggest that shape effects in a reflexive spatial attention paradigm are predominantly mediated by dorsal stream areas.

As seen in Fig. 5, shape pair LIP$_{max-dissimilar}$, the shape pair that is encoded most dissimilarly in LIP, produces consistent effects across CTOAs up to 450 ms. Shape pair LIP$_{max-dissimilar}$ was able to produce inhibitory shape effects that were significantly larger than shape effects for the control shape pairs (Fig. 6A). Additionally, the lack of a difference in the shape effect between the AIT$_{max-dissimilar}$ and the control shape pair further suggests that ventral stream areas did not significantly modulate these reflexive shape effects on spatial cueing.

The shape distances used in the present study were obtained from the Lehky and Sereno (2007) monkey study, which used a passive fixation task. The present study uses a modified reflexive spatial attention task with localization response. Hence, there are task differences between these two studies, which raises a question of whether shape distances computed from a fixation task can be applied to a reflexive attention task. First, in the present study we are not comparing across these different tasks. We take from Lehky and Sereno (2007), the neural population distances between shapes in two different cortical areas to create sets of stimuli that are more distinctive in one cortical area versus the other.

Table 7
Mean RTs of first five CTOAs for each shape pair.

Shape pair	Cued (ms)				Uncued (ms)			
	Same shape		Different shape		Same shape		Different shape	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
AIT$_{max-dissimilar}$	307.0	1.3	305.5	1.3	286.3	1.3	287.0	1.3
LIP$_{max-dissimilar}$	306.5	1.3	299.9	1.3	280.2	1.3	281.3	1.3
Control	308.8	0.9	306.3	0.9	286.0	0.9	286.6	0.9

Second, in both studies (and tasks), shape is behaviorally irrelevant. In the Lehky and Sereno paper, the animal performed a passive fixation task, where shape of the stimulus was behaviorally irrelevant. In the present study that employs a spatial attention paradigm, shape is again behaviorally irrelevant. Third, in the present study, we keep task constant (spatial attention task) and vary only the shapes of the cue and target, based on this monkey physiology. Because RTs are derived from the endpoint of a complicated hierarchical process that includes sensory (visual), attentional (executive) and response (motor) related factors, we were careful in our study to keep these factors constant across conditions and vary only the shape distances in our sets of stimuli. Hence, it is of utmost importance to note that across all the tested conditions there were no task differences in our design. That is, given that the task was constant across our stimulus pairs, it could not explain the differences between shape pairs that we report. Fourth, although we are not aware of neurophysiological studies that have carefully examined whether shape encoding is constant across behavioral task, a few studies have examined or discussed this issue and report that there is consistency of a cell's shape selectivity across a passive fixation and delayed match-to-sample tasks, even when comparing across tasks where shape was behaviorally irrelevant versus relevant (Peng et al., 2008, pp. 803–804; see also Sereno & Amador, 2006, Fig. 4). Yet, it is possible that the shape distances themselves would somehow vary with task (passive fixation task versus reflexive spatial attention task conditions). If shape distances either increased or decreased with the current task, this would simply amplify or dampen differences we report. Only if one assumes that this change in task (fixation versus localization) affected shape encoding in one cortical area differently than the other, could it present a problem of interpretation for the present study. We think that although such a scenario may be theoretically possible, given that shape was behaviorally irrelevant for both tasks, it is unlikely.

As reviewed in the introduction, coding of shape in human and monkey IT has been recently shown to be very similar using stimuli similar to those employed in the present study (Kriegeskorte, 2009; Kriegeskorte et al., 2008). Further, monkeys and humans also perform similarly in categorization tasks (Fize, Cauchoix, & Fabre-Thorpe, 2011; Sigala, Gabbiani, & Logothetis, 2002), consistent with the idea of both species having very similar visual representations. While studies have noted differences in the number of anatomical regions exhibiting shape sensitivity in IPS for monkeys compared to humans (Orban et al., 2006) specific studies that directly compare shape encoding in the parietal cortex of human and monkey have not been performed. Further, it remains possible that some aspect of shape encoding in the dorsal and ventral systems of humans is not similar to that of monkeys. If so, the slowed responses for the LIP$_{max-dissimilar}$ pair could be the result of some other aspects or characteristics of these stimuli that are specific to human visual representations (and not monkey) that make this particular pair more dissimilar than the other pairs, thus resulting in a larger shape effect. Such a scenario would suggest that it is not dorsal stream shape selectivity, per se, that is responsible for the findings, but rather a specific increase in the distinctiveness of this

shape pair in humans compared to monkeys that resulted in this pattern of findings. Given the recent reported similarities in coding of shape between the species using a range of visual stimuli, we think this scenario unlikely.

It is important to note that the present findings are obtained in a reflexive spatial cueing paradigm without shape or spatial expectancies. We presume that shape effects could be different for similar tasks that involve voluntary attention (Bengson & Mangun, 2011; Kingstone, 1992; Mattler, 2004). Finally, although the present findings suggest that dorsal stream is dominating shape effects in this reflexive spatial cueing paradigm, it is possible that under different task conditions, such as tasks that require discrimination or identification of the target, these shape similarity effects may depend instead more heavily on ventral stream encoding of shape (Walsh et al., 1992). Thus, the unique shape encoding in the dorsal stream may be most pronounced in tasks that embody dorsal functions, such as a reflexive spatial attention task. These findings are a critical first step in trying to better understand why shape selectivities are represented in both cortical visual streams and what functions these different shape encodings subserve.

5. Conclusion

In summary, recent work (Patel, Peng, & Sereno, 2010; Sereno et al., 2010) suggests that repetition suppression and mutual inhibition are key mechanisms responsible for spatial attentional effects. In that model, those two mechanisms can explain why and how shape may influence these spatial attentional effects. Recent physiological and imaging studies, in monkeys (Janssen et al., 2008; Sereno & Maunsell, 1998; Sereno, Trinath, Augath, & Logothetis, 2002) and in humans (Konen & Kastner, 2008), have demonstrated that shape is processed in both ventral and dorsal visual streams. In a first comparison of shape encoding across streams in the monkey, Lehky and Sereno (2007) demonstrated a distinct neural encoding of shape for a small set of highly controlled 2D shapes. Using these shapes and these documented physiological shape encoding differences, we show here that the shape effects in reflexive spatial attention appear to be mediated by dorsal, and not ventral stream, shape encoding. Even though ventral stream areas such as AIT are normally implicated in the analysis of shape, the analysis and usage of shape information may depend on the task at hand. That is, shape effects in a localization task, but perhaps not identification task, may depend on dorsal selectivities. These findings are a first step towards understanding why there exist separate (possibly parallel) shape encoding in ventral and dorsal streams and are supportive of the idea that they subserve different functions. Specifically, we show here that the shape encoding that occurs in populations of dorsal stream cells appears to mediate reflexive spatial attention in localization tasks.

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