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Exogenously cued attention triggers competitive selection of surfaces

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Abstract

It has been reported that when an endogenous cue directs attention to a brief translation of one of two superimposed surfaces, observers reliably report the direction of that translation as well as the direction of a second translation of the cued surface. In contrast, if the uncued surface translates second, direction judgments are severely impaired for several hundred milliseconds. We replicated this result, but found that the impairment survived the removal of the endogenous cue. The impairment is therefore not due to endogenously cued attention. Instead, a brief translation of one surface acts as an exogenous cue that triggers an automatic selection mechanism, which suppresses processing of the other surface. This study provides a clear case of exogenous cueing of surface-based attention. We relate these results to identified competitive selection mechanisms in visual cortex.

Keywords: Attention; Cortex; Object; Competition; Attentional blink

1. Introduction

Valdes-Sosa, Cobo, and Pinilla (2000) recently introduced an ingenious paradigm to examine surface-based attention, isolated from the influence of feature-based or spatial attention. On each trial, observers viewed two random dot patterns (one red, one green) that rotated around a common center in opposite directions (see Fig. 1). The fixation point color (red or green) acted as an endogenous cue that directed subjects to attend to the surface of the corresponding color. After a brief delay, the cued surface translated briefly in one of eight directions while the uncued surface continued to rotate. After this translation, both surfaces rotated until one of the two surfaces, selected at random with equal probability, underwent a second brief translation. On each trial, observers reported the directions of the two shifts. The endogenous cue indicated which surface would shift first so observers could ignore one surface in order to reliably report the first shift. The endogenous cue provided *no* information about which surface would translate second, requiring the observer to divide attention between the two surfaces to report the second translation.

Subjects were able to report the first translation accurately, and could also report the second translation of the *cued* surface accurately even when two successive translations occurred with an interstimulus interval (ISI) as short as 150 ms. If the *uncued* surface translated second, however, judgments were severely impaired, and this impairment lasted ≈600 ms.

We questioned the role of the endogenous cue in these attentional effects. We noted that the first translation always occurred on the endogenously cued surface. This suggested that the observed impairment might be attributable, not to endogenously directed attention, but to the first translation acting as an exogenous cue. To test this hypothesis, we repeated the original experiment but removed the endogenous cue by replacing the colored fixation point with a non-informative gray fixation point. As described below, the removal of the endogenous cue had only a small effect on performance. A similar pattern of performance was observed when delayed onset of one surface was used as an exogenous cue. Thus, in Valdes-Sosa's original paradigm, the impairments in judging the second translation were caused

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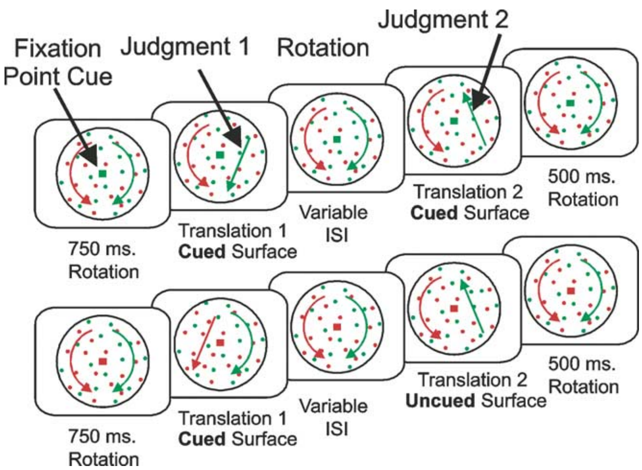

Fig. 1. Task. Panels are arranged from left to right according to the sequence of events in each trial. One half of all trials were cued trials, in which the fixation point color (green as in upper panels or red as in lower panels) indicated which surface would translate first. Following a 750 ms period of rotation, the cued surface then translated for 150 ms in one of the eight cardinal directions, while the other surface continued to rotate. The two surfaces then continued to rotate for a variable delay of 150–1050 ms, at which point one of the two surfaces, chosen with equal probability, shifted for 150 ms. After this second shift, both surfaces rotated for an additional 500 ms. Observers had to maintain fixation throughout the trial, and report the direction of each shift. The remaining trials were uncued trials (not shown), in which the fixation point was gray and provided no information about which surface would translate first. Cued and uncued trials were intermixed at random. Experiment 3 was identical to Experiments 1 and 2 except as follows. The first translation was eliminated, and observers reported the sole remaining translation. The fixation point was always a non-informative gray, and one of the surfaces appeared first, followed, after 750 ms, by the appearance of the second surface. The two surfaces continued rotating for a variable ISI, after which one surface, selected at random, translated while the other surface continued to rotate. After this translation, both surfaces rotated for 500 ms. Observers had to maintain fixation throughout the trial, and report the direction of the single shift.

primarily, not by the endogenous cue, but by the first translation acting as an exogenous cue. These experiments offer the first clear example of exogenously cued surface-based attention.

2. Methods

2.1. Stimuli and task

All experiments were conducted in a dark quiet room. Equiluminance between red and green guns was established for each subject using heterochromatic flicker fusion (Ives, 1912), with a flicker rate of 60 Hz. The red gun was held constant at maximum intensity and the green gun was adjusted until minimal flicker was reported. This procedure was repeated eight times and the results averaged. For each subject the resulting gun values were used throughout the remainder of the experiment.

For the first session, subjects were given verbal instructions and practiced the task. Data from this practice session were discarded, and all analysis was performed only on data collected after the first session. An experimenter sat with the subject throughout every session to ensure that eye fixation monitoring was accurate. Subjects were allowed to pause and rest at any time they felt fatigued. Except during these pauses, they sat comfortably 57 cm from the computer monitor, with head resting in a chin and forehead rest, to stabilize the head for eye position monitoring. Eye position was continuously monitored using an ISCAN Model ETL-400 infrared eye tracking system, operating at a 60 Hz sampling rate (ISCAN, Inc. Burlington, MA). Fixation breaks occurred on 13.5% of all trials, and these trials were excluded from further analysis. None of the subjects showed a significant difference across cueing conditions in rate of fixation breaks, according to a chi-squared test, $p < 0.05$.

2.1.1. Experiments 1 and 2

At the beginning of each trial, a fixation point (0.3×0.3 deg of visual arc) appeared at the center of a computer monitor (Trinitron Multiscan TC, operating at 60 Hz). After achieving fixation within a 1-deg square window observers initiated trials by key-press. Pressing the key caused two overlapping random dot patterns (one red, one green) to appear. The dot density of each dot field was 5 dots per square degree of visual arc. Stimuli were viewed through a circular aperture 2.75 deg in diameter. Each dot subtended 0.05 deg of visual arc. These two dot patterns rotated rigidly in opposite directions around the fixation point, with red dots rotating clockwise on half the trials and green dots rotating clockwise on the other half of the trials. Both patterns rotated 50 deg per second. These two patterns of dots gave rise to the percept of two superimposed rigid transparent surfaces, covered with red and green dots (see Fig. 1).

On half of the trials, the fixation point color (red or green) cued subjects to attend to the surface of the corresponding color. Subjects were informed that, on these trials, the surface indicated by the cue would always translate first. On the remaining half of trials, the fixation point was gray and therefore provided no information about which surface would translate first. Subjects were informed that, in this case, either surface would translate first, with equal probability. The two trial types were randomly interdigitated.

Every trial began with a 750-ms period during which both populations of dots continuously rotated. After this period of rotation, one of the surfaces (the cued one if an endogenous cue was present) underwent a brief

(150 ms) shift in one of eight directions while the uncued surface continued to rotate. As in the original study of Valdes-Sosa and colleagues, 60% of the dots translated coherently, while the remaining 40% of dots moved randomly in the remaining seven directions. This discouraged subjects from solving the task by attending to individual dots. All dots translated at a speed of 1.2 deg of visual arc per second.

At the end of this translation, both surfaces rotated for a variable period of time, selected randomly with equal probability from five possible ISI's (150, 300, 450, 800 or 1050 ms). At the end of this rotation, one or the other surface, with equal probability, translated for 150 ms, followed by a period of 500 ms during which both surfaces resumed rotation, thereby masking the second translation. On each trial, observers reported the directions of the two shifts, by pressing the key in the corresponding position around a numeric keypad. Observers were allowed to report the direction of each shift as soon as it occurred, but were required to maintain fixation within a 1-deg fixation window throughout the trial. Breaks of fixation, incorrect responses, and correct responses were signaled immediately by one of three different computer generated sounds.

2.1.2. Experiment 3

Experiment 3 tested whether the observed pattern of performance required discrimination of the first translation, or could be induced by a cue that required no discrimination. The design of this experiment was identical in all respects to Experiments 1 and 2, except as follows. The fixation point was always gray, and provided no information about which surface would translate. When a key press initiated a trial, one of the dot patterns, selected at random with equal probability, appeared and rotated either clockwise or counterclockwise. After a delay of 750 ms, the other dot pattern appeared, rotating in the opposite direction. The pair of surfaces continued rotating for a variable period of time (ISI's: 150, 300, 450, 800 or 1050 ms), selected at random with equal probability. After this period of rotation, one of the surfaces (again selected at random with equal probability) translated in one of eight directions, while the other surface continued to rotate. Following this translation, both surfaces rotated for 500 ms. Subjects were required to report the direction of the sole translation. In order to compare performance in this task with performance in Experiments 1 and 2, we set the translation duration for each individual subject to a value at which their mean accuracy in judging the direction of translation of the delayed onset (cued) surface was similar to the mean accuracy in judging the cued surface in Experiments 1 and 2 (60–70%). This value was determined at the beginning of each subject's first recording session in Experiment 3.

2.2. Observers

Experiments were undertaken with the understanding and written consent of each subject. All observers were paid to participate in the experiment. All had normal or corrected to normal vision. All subjects were naïve as to the purpose of the experiment. Ages ranged from 17 to 21 years. Eight subjects participated in Experiments 1 and 2. Of these, six were women and two were men. Five subjects participated in Experiment 3. Of these, two were women and three were men.

3. Results

3.1. Experiment 1: endogenously cued attention

Subjects ran between 960 and 1280 trials (mean, 1030 trials), yielding a mean of 56 repetitions (standard deviation, 7.4) in each of the 20 experimental conditions (five ISI's; successive translations on either the same or different surfaces; two cueing conditions: gray fixation point or else colored fixation point acting as an endogenous cue).

In close agreement with the findings of Valdes-Sosa et al. (2000), subjects were able to report both translations of the cued surface accurately, even when they occurred within 150 ms of one another, but were severely impaired in judging translations of the uncued surface. Fig. 2 shows average performance across subjects. Data are arranged according to the length of the ISI. By convention, negative ISI's correspond to judgments of the first translation and positive ISI's correspond to judgments of the second translation. Subjects accurately judged first translations of the cued surface (left side of graph), and second translations of the cued surface (black line, right side of graph). In contrast, subjects were severely impaired in judging second translations if they were of the uncued surface (gray line, right side of graph).

3.2. Experiment 2: removal of endogenous cue

To test whether this impairment in judging translations of the uncued surface was caused by the endogenous cue, we randomly intermixed trials in which the fixation point was gray, and therefore did not cue either surface. Performance in this task is illustrated in Fig. 3. Accuracy in judging the *first* translation was better with the endogenous cue than without, indicating that subjects did benefit from the endogenous cue (mean accuracy = 74.2% with cueing, 65.1% without, a difference that was highly significant: $p < 0.0001$, three-way ANOVA with ISI, Cue vs. No-cue and same vs. different surfaces as factors). However, a comparison of judgments of the *second* translation on trials with and without an endogenous cue revealed a remarkably similar pattern of performance. On trials in which the fixation point was gray, observers were still severely impaired in second translation judgments when first one, and then the other surface translated. This impairment was not significantly different from that observed on endogenously cued trials, according to a three-way ANOVA, with ISI, cue vs. no-cue and same vs. different surface as factors (no effect of cueing or interaction between cueing and other variables $p > 0.05$). As was the case on endogenously cued trials, this impairment was observed at the shortest ISI tested (150 ms), and declined at longer ISI's. Judgments of the second translation of the same surface were comparable across the two conditions (mean accuracy 65.4% with cue, 62.6% without cue).

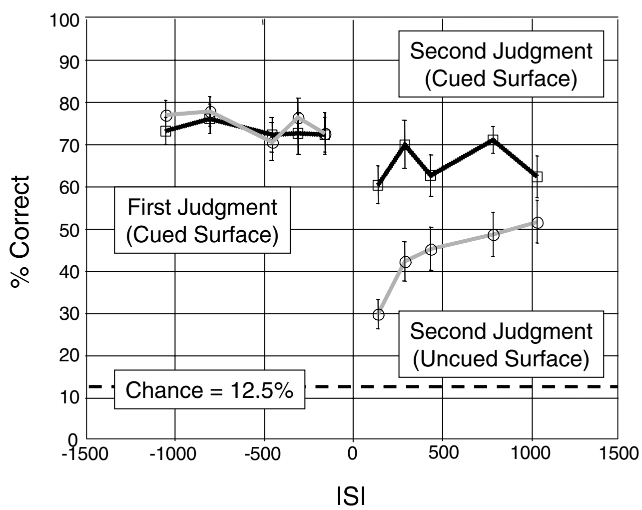

Fig. 2. Mean accuracy across eight subjects in reporting the direction of two successive translations, averaged across trials in which the fixation point color indicated which surface would translate first. Chance performance, indicated by dashed horizontal line, was 12.5%. ISI indicates the duration of the interval between the offset of the first translation and the onset of the second translation. By convention, negative ISI's correspond to judgments of the first translation, and positive ISI's correspond to judgments of the second translation. Thus, points at –1050 correspond to accuracy in judging the first translation, averaged across trials when the two translations were separated by an ISI of 1050 ms. Points at +1050 correspond to the second judgment, averaged across the same trials. Line color indicates whether the first and second translations occurred on the same surface (black) or different surfaces (gray). Error bars indicate standard errors of mean (SEM) performance across subjects. Observers accurately reported the direction of the first translation (which was always on the surface cued by the fixation point), regardless of whether the second translation also occurred on the cued surface (black line) or occurred on the other surface (gray), and regardless of how soon after the first translation the second translation occurred. Subjects also reported the second translation accurately if it occurred on the cued surface. However, subjects were severely impaired in making judgments about the second translation when it occurred on the uncued surface. This impairment was greatest at the shortest ISI tested (150 ms) and gradually diminished over time.

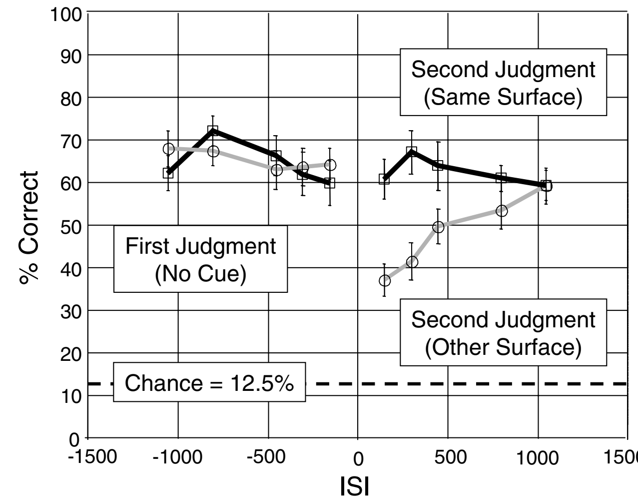

Fig. 3. Mean accuracy across eight subjects in reporting the direction of two successive translations for trials in which the fixation point was gray. Conventions are identical to those used in Fig. 2. Despite the absence of the endogenous cue, observers were able to report the direction of the first translation on 65.1% of trials, and their performance did not depend on whether the second translation also occurred on the cued surface (black line) or occurred on the other surface (gray line), and did not depend on ISI. Subjects reported the second translation accurately if the same surface translated twice. However, if one surface, then the other, translated, this severely impaired the observers' ability to report the second translation. As was the case in the cued condition, this impairment was greatest at the shortest ISI's tested (150 ms) and gradually diminished over time.

3.3. Experiment 3: delayed onset as an exogenous cue

This impairment might depend on the subject making a judgment about the first translation. When observers discriminate one stimulus, this momentarily impairs discrimination of subsequently presented stimuli, a phenomenon known as the attentional blink (see, e.g., Shapiro, Raymond, & Arnell, 1994). The time course of the attentional blink is similar to that of the impairment observed in Experiments 1 and 2. Alternatively, the impairment could simply be due to the first translation acting as an exogenous cue. To test this, we replaced the first translation with an exogenous cue that did not require a perceptual judgment: the abrupt onset of one of the two surfaces. Abrupt stimulus onset has been found, in other contexts, to be a potent exogenous cue (Yantis & Jonides, 1984, 1990). On each trial, one of the two surfaces appeared first, and rotated for 750 ms before the second surface appeared. After this abrupt onset, both surfaces rotated for a variable period of time (ISI's: 150, 300, 450, 800 or 1050 ms), and then one of the two surfaces, selected at random, translated.

Observers were substantially better at judging the direction of translation of the new (cued) surface than the old (uncued) surface. This is illustrated in Fig. 4, which shows mean accuracy on the new surface (black line) and the old surface (gray line). The difference in

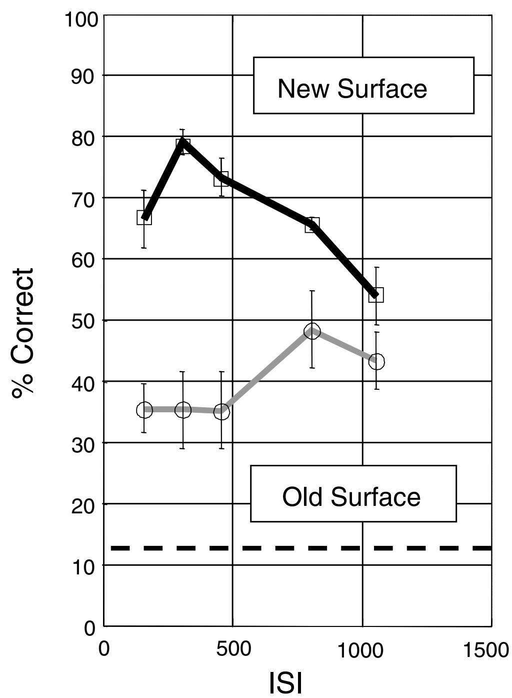

Fig. 4. Mean accuracy across five subjects in reporting the direction of the translation in the delayed onset task. The black line indicates mean accuracy in judging translation of the new (cued) surface as a function of the interval between the appearance of the new surface and the onset of translation. The gray line indicates mean accuracy in judging the translation of the old (uncued) surface, again as a function of the interval between the appearance of the new surface and the onset of translation. Chance performance was 12.5%, and is indicated by the dashed line. Old surface judgments were impaired relative to those of the new surface.

performance was highly significant (two-way ANOVA with ISI and old vs. new surface as factors, main effect of surface, $p < 0.0001$), and depended on ISI (interaction of ISI and surface, $p = 0.0046$). Despite the fact that the task differed in the number of judgments to be made and the mode of exogenous cueing, the time course of the impairment is qualitatively similar to that observed in the first two experiments.

4. Discussion

4.1. Summary

These results demonstrate that attention can be cued exogenously to one of two surfaces, and that this cueing impairs processing of the uncued surface. Following a brief translation of one surface, observers were severely impaired in making judgments about translations of the other surface. This impairment occurred quite rapidly, manifesting itself at the shortest ISI tested (150 ms) and lasted for hundreds of milliseconds. This type of impairment was also observed on trials in which the subject was endogenously cued to attend to the surface that underwent the first translation. However, the impairment survived the removal of this endogenous cue, suggesting that the effect was due to the first translation acting as an exogenous cue. Consistent with this interpretation, a similar pattern of performance was observed when the first translation was removed, and one of the surfaces was cued instead by delaying its appearance by 750 ms. The two surfaces were superimposed spatially, so these results cannot be attributed to spatial exogenous orienting mechanisms. Rather, the results are consistent with a model in which the neurons that are driven by the two surfaces automatically compete with one another, with the neurons responding to the exogenously cued surface temporarily winning the competition.

4.2. Ruling out spatial and feature-based attention

Some of the clearest evidence for surface-based attention comes from studies in which visual stimuli have been superimposed. This approach rules out explanations based on purely spatial attention mechanisms. The psychophysical paradigm developed by Valdes-Sosa and colleagues, which we have adopted in a slightly modified form in the present study, has several advantages over related studies of object-based attention that have similarly controlled for spatial attention by superimposing stimuli (Duncan, 1984; O'Craven, Downing, & Kanwisher, 1999). First, the eight different directions of translation that were discriminated in the present paradigm are identical across the two surfaces. The attentional effects cannot therefore be attributed to modulation of the gain of motion channels such as have been reported in a single-unit recording study of feature-based attention in area MT (Treue & Martinez Trujillo, 1999) and in an fMRI study of attention in humans (Saenz, Buracas, & Boynton, 2002). The two surfaces were viewed through the same virtual aperture, eliminating the possibility that the observed effects could result from a different distribution of resources in space, a criticism leveled against Duncan (1984) by Kramer and Jacobson (1991). Finally, the dots defining the two surfaces in the present paradigm were drawn from the same probability distribution, so any differences in the spatial frequency content of the two surfaces are minimal, arguing against modulation of frequency filters as a potential selection mechanism, a possibility that was raised with regard to the study of Duncan (1984) by Watt (1988) and which also applies to several other recent studies.

4.3. Explanations based on divided attention and dwell time

Previous results of experiments under conditions equivalent to the endogenously cued condition in the present experiment were interpreted as arising from the limited capacity of the visual system to process information about multiple objects (Valdes-Sosa et al., 2000). In those experiments, as in our own, subjects accurately reported the first translation, but were impaired in judging the second translation if it involved the uncued surface. According to the interpretation offered by the authors, the endogenous cue enabled observers to attend to one of the two surfaces and their performance for the first translation was therefore high. However, either surface could undergo the second translation with equal probability, and therefore, observers had to divide attention between the two surfaces. The extra cost of attending to two objects caused their performance on the second judgment to be poorer, on average, than their performance on the first judgment. The observation that this reduction in performance occurred primarily when judgments were of the surface that was not endogenously cued was attributed to the initial allocation of attention to the endogenously cued surface. As Valdes-Sosa et al. (2000) noted, Duncan, Ward, and Shapiro (1994) have found that attention remains attached to a stimulus for several hundred milliseconds, during which time judgments of other stimuli are impaired.

The present experiments provide two insights that require this explanation to be refined. First, if the surface-dependent difference in the accuracy of second translation judgments were due to the slow withdrawal of endogenously cued attention, then this performance difference should have disappeared when the endogenous cue was removed. Instead, we found that the surface-dependent impairment persisted after removal of the endogenous cue. In fact, removal of the endogenous cue had no statistically significant effect on second judgment accuracy. Second, our results do not support the proposal that the impairment resulted from an intrinsic inability to attend simultaneously to both surfaces. If lower mean accuracy in judging the second translation were due to the need to divide attention between the two surfaces, then first translation judgments should have been severely impaired when the endogenous cue was removed. Removal of the endogenous cue had only a mild effect on the mean accuracy of first translation judgments, indicating that subjects could easily divide attention across the two surfaces to report a translation of either surface. Mean accuracy of uncued second translation judgments was substantially poorer than accuracy on uncued first translation judgments, a difference that cannot be attributed to the need to divide attention, which was required in both cases. Taken together, these findings show that impairments in judging the second translation cannot be explained by the endogenous cue or the requirement to divide attention between two surfaces.

4.4. *Possible neuronal mechanisms of surface-based attention*

The results can, perhaps, be understood as resulting from the operation of competitive circuits in visual cortex. Single unit recording studies and lesion studies of spatial attention in awake, behaving monkeys have found that when multiple stimuli appear simultaneously in the visual field, they activate populations of neurons in extrastriate visual cortex that mutually inhibit one another, both in dorsal processing areas that process information about stimulus motion (Recanzone & Wurtz, 2000; Recanzone, Wurtz, & Schwarz, 1997) and in ventral areas that process information about the form and identity of objects (Chelazzi, Miller, Duncan, & Desimone, 1993; Luck, Chelazzi, Hillyard, & Desimone, 1997; Reynolds, Chelazzi, & Desimone, 1999). This competition occurs automatically, in that competitive interactions are observed among unattended stimuli, when the monkey is attending elsewhere to perform a difficult task (Reynolds et al., 1999). Competition among unattended stimuli is resolved in favor of the more salient stimulus (Reynolds and Desimone, Society for Neuroscience Abstracts, 23:122.9).

Therefore, a parsimonious explanation for the impairment in the present experiment is that the transient neuronal responses induced by the first translation (Experiments 1 and 2) and by the onset of the delayed surface (Experiment 3) put neurons that responded to the cued surface at a competitive advantage over neurons that were activated by the uncued surface. This model provides an explanation for a curious aspect of the subjects' behavioral performance. Given their relatively high performance in judging the first uncued translation, an ideal strategy would have been for subjects to treat the second translation as a completely new event, identical to the first. If they were able to do so, they could have judged the second translation as accurately as they judged the first. The fact that they could not avoid being impaired in the second judgment when different surfaces underwent successive translation seems to be an important signature of an underlying neural mechanism. This sub-optimal pattern of performance would be expected if the first translation triggered the automatic resolution of competition in favor of the translating surface. Thus, while our results do not support the proposal that the impairment reflects an inherent inability to simultaneously process both surfaces, they do support the proposal that competition introduces a *temporary* impairment in processing the uncued surface.

All previous neurophysiological studies that have examined attentional modulation of these competitive circuits have used stimuli that appeared at separate locations. It is therefore unknown whether these circuits mediate competition between neurons with different receptive field locations or between neurons encoding the properties of pre-attentively integrated objects. The present results suggest that these extrastriate circuits may mediate selection, not only of stimuli at different spatial locations, but of objects or surfaces, even when they are spatially superimposed.

4.5. Transparent motion and competitive interactions

Psychophysical and single-unit recording studies of transparent motion are also indicative of neuronal competition. Under ordinary viewing conditions, two superimposed moving patterns are both quite discernable, corresponding to the well-known phenomenon of "motion transparency". Adding a second moving pattern, however, does make both patterns less detectable (e.g. Lindsey & Todd, 1998; Mather & Moulden, 1983; Snowden, 1989; Verstraten, Fredericksen, van Wezel, Boulton, & van de Grind, 1996). This psychophysical phenomenon is mirrored by directionally selective neurons within cortical area MT which, when a second stimulus is superimposed, give a reduced response to a stimulus moving in their preferred direction (Snowden, Treue, Erickson, & Andersen, 1991; Qian & Andersen, 1994). Taken together these observations imply the existence of mutually inhibitory connections between direction selective neurons.

Given these inhibitory connections, it seems plausible that the onset of a moving pattern would, due to the neuronal onset transient, temporarily tip the competitive balance in favor of the neurons encoding the *direction* of that pattern. However, it is not immediately clear whether, and if so, how, direction-specific inhibitory connections could lead to the *surface*-specific perceptual impairments we (and Valdes-Sosa et al. before us) observed—subjects are impaired, not in judging a particular direction of motion, but in judging any translation of the uncued surface.

This mystery has, however, been made more approachable by our discovery that surface-based attention can be elicited by an exogenous cue. In particular, our discovery that surface-based attention can be cued exogenously has enabled us to measure the influence of exogenous cues on competitive interactions in extrastriate cortex of the monkey. We have found that an exogenous cue causes the cued stimulus to dominate neuronal responses with a time course comparable to that of the perceptual impairments observed in the present study (Fallah, et al. Society for Neuroscience 418.5). By pursuing these neurophysiological investigations, in conjunction with modeling of competitive neuronal networks, we hope to understand the neuronal mechanisms underlying surface-based attention.

4.6. Exogenously vs. endogenously cued surface-based attention

Exogenous cueing has been studied extensively in the context of spatial attention, and is often assumed to be the result of spatially selective orienting mechanisms. However, several recent studies have examined exogenous cueing of attention to objects. Egly, Driver, and Rafal (1994) used a brief flash to cue one end of a bar and found that observers were faster at detecting a change at the uncued end of the cued object than they were at detecting an identical change appearing at an equidistant location on a different object. However, because the cue was 75% valid, it served both as an endogenous and as an exogenous cue and therefore the relative contributions of the two types of cues is unclear. In addition, Tipper, Driver, and Weaver (1991) have used exogenous cueing in a study that provided evidence of "inhibition of return" (Posner & Cohen, 1984) in the context of object-based attention. We believe, however, that our study is the first to demonstrate exogenous surface-based cueing for superimposed stimuli. As observed above, the use of superimposed stimuli rules out spatial attention.

The endogenous cue had only a relatively mild effect on behavior in the present paradigm, reflected in slightly improved performance in judging the first translation when the endogenous cue indicated which surface would translate first. Our results do not, however, argue against the possibility of endogenously cued object-based attention. In fact, using stimuli quite similar to those used in the present study, Valdes-Sosa, Cobo, and Pinilla (1998) has provided evidence that coherent surfaces can be selected by attention in the absence of an exogenous cue.

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References

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature, 363*(6427), 345–347.

Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General, 113*(4), 501–517.

Duncan, J., Ward, R., & Shapiro, K. (1994). Direct measurement of attentional dwell time in human vision. *Nature, 369*, 313–315.

Egly, R., Driver, J., & Rafal, R. D. (1994). Shifting visual attention between objects and locations: evidence from normal and parietal lesion subjects. *Journal of Experimental Psychology: General, 123*(2), 161–177.

Ives, H. E. (1912). On heterochromatic photometry. *Philosophical Magazine, 24*, 845–853.

Kramer, A. F., & Jacobson, A. (1991). Perceptual organization and focused attention: the role of objects and proximity in visual processing. *Perception and Psychophysics, 3*, 267–284.

Lindsey, D. T., & Todd, J. T. (1998). Opponent motion interactions in the perception of transparent motion. *Perception and Psychophysics, 60*(4), 558–574.

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology, 77*(1), 24–42.

Mather, G., & Moulden, B. (1983). Thresholds for movement direction: two directions are less detectable than one. *Quarterly Journal of Experimental Psychology A, 35*(3), 513–518.

O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature, 401*(6753), 584–587.

Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. Bouwhuis (Eds.), *Attention and performance* (*Vol. X*, pp. 531–556). Earlbaum.

Qian, N., & Andersen, R. A. (1994). Transparent motion perception as detection of unbalanced motion signals. II. Physiology. *Journal of Neuroscience, 12*, 7367–7380.

Recanzone, G. H., & Wurtz, R. H. (2000). Effects of attention on MT and MST neuronal activity during pursuit initiation. *Journal of Neurophysiology, 83*(2), 777–790.

Recanzone, G. H., Wurtz, R. H., & Schwarz, U. (1997). Responses of MT and MST neurons to one and two moving objects in the RF. *Journal of Neurophysiology, 78*(6), 2904–2915.

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *Journal of Neuroscience, 19*(5), 1736–1753.

Saenz, M., Buracas, T. S., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience, 5*(7), 631–632.

Shapiro, K. L., Raymond, J. E., & Arnell, K. M. (1994). Attention to visual pattern information produces the attentional blink in RSVP. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 357–371.

Snowden, R. J. (1989). Motions in orthogonal directions are mutually suppressive. *Journal of the Optical Society of America [A], 7*, 1096–1101.

Snowden, R. J., Treue, S., Erickson, R. G., & Andersen, R. A. (1991). The response of area MT and V1 neurons to transparent motion. *Journal of Neuroscience, 9*, 2768–2785.

Tipper, S. P., Driver, J., & Weaver, B. (1991). Object-centred inhibition of return of visual attention. *Quarterly Journal of Experimental Psychology A, 43*(2), 289–298.

Treue, S., & Martinez Trujillo, J. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature, 399*(6736), 575–579.

Valdes-Sosa, M., Cobo, A., & Pinilla, T. (1998). Transparent motion and object-based attention. *Cognition, 66*(2), B13–B23.

Valdes-Sosa, M., Cobo, A., & Pinilla, T. (2000). Attention to object files defined by transparent motion. *Journal of Experimental Psychology: Human Perception and Performance, 26*(2), 488–505.

Verstraten, F. A., Fredericksen, R. E., van Wezel, R. J., Boulton, J. C., & van de Grind, W. A. (1996). Directional motion sensitivity under transparent motion conditions. *Vision Research, 36*(15), 2333–2336.

Watt, R. J. (1988). *Visual processing: computational, psychophysical and cognitive research*. Hillsdale, NJ: Erlbaum.

Yantis, S., & Jonides, J. (1984). Abrupt visual onsets and selective attention: evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance, 10*(5), 601–621.

Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance, 16*(1), 121–134.