

Ground-based inhibition: Suppressive perceptual mechanisms interact with top-down attention to reduce distractor interference

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Successful attentional function requires inhibition of distracting information (e.g., Deutsch & Deutsch, 1963). Similarly, perceptual segregation of the visual world into figure and ground entails ground suppression (e.g., Likova & Tyler, 2008; Peterson & Skow, 2008). Here, we ask whether the suppressive processes of attention and perception—distractor inhibition and ground suppression—interact to more effectively insulate task performance from interfering information. We used a variant of the Eriksen flanker paradigm to assess the efficacy of distractor inhibition. Participants indicated the right/left orientation of a central arrow, which could be flanked by congruent, neutral, or incongruent stimuli. We manipulated the degree to which the ground region of a display was suppressed and measured the influence of this manipulation on the efficacy with which participants could inhibit responses from incongruent flankers. Greater ground suppression reduced the influence on target identification of interfering, incongruent information, but not that of facilitative, congruent information. These data are the first to show that distractor inhibition interacts with ground suppression to improve attentional function.

Introduction

Our visual world is filled with information, only a small fraction of which is relevant to our current goals.

Because our capacity to represent and respond to this information is limited, we continuously modulate our representations of the visual environment. Representations relevant to the task at hand are enhanced, while those that distract from task performance are inhibited. The term “attention” refers to this selective process. For instance, when selecting information from a specific region of space, visual feature and object type speeds any responses to and increases extrastriate signal evoked by the selected stimuli (e.g., Chawla, Rees, & Friston, 1999; B. A. Eriksen & Eriksen, 1974; Müller & Kleinschmidt, 2003; O’Craven, Downing, & Kanwisher, 1999; Posner, 1980). Likewise, extrastriate signal to stimuli that must be disregarded is suppressed (e.g., Gazzaley et al., 2007; Ruff & Driver, 2006). Attention, then, modulates the representations of visual stimuli to determine which information will guide behavior.

Because visual attention acts on and through the functional architecture that supports visual perception, it is reasonable to suppose that these two functions, classically considered independent, in fact continuously modulate one another (e.g., Franconeri, Alvarez, & Cavanagh, 2013; McMains & Kastner, 2011; Scalf, Basak, & Beck, 2011; Scalf & Beck, 2010; Scalf, Torralbo, Tapia, & Beck, 2013). Single-cell, behavioral, and neuroimaging evidence indicate that attentional enhancement is indeed modified by the perceptual segregation of the visual scene into objects (e.g., Driver & Baylis,

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1989; Duncan, 1984; Egly, Driver & Rafal, 1994; McMains & Kastner, 2011; Qiu, Sugihara, & von der Heydt, 2007). During figure–ground segmentation, potential objects on opposite sides of a border compete for figural status; the winner of this competition is perceived as the object, while the loser is seen as shapeless ground (e.g., Grossberg, 1994; Kienker, Sejnowski, Hinton, & Schumacher, 1986; Peterson & Skow, 2008). This competitive interaction has direct consequences for attentional enhancement (Qiu et al., 2007). Directing attention into the receptive field of V2 neurons increases their firing rate. This amplification interacts with the figural status of the information being coded by those neurons, such that attention causes a disproportionately large increase in signal from V2 cells that are responding to figural rather than ground regions of the display (Qiu et al., 2007); this is a multiplicative effect. In humans, the signal enhancement that results from visual items forming a figure reduces the amount of top-down attention required to detect a slight change in luminance (McMains & Kastner, 2011). Furthermore, directing top-down attention to one region of a figure increases the signal evoked by its other unattended regions (Martinez et al., 2006; Müller & Kleinschmidt, 2003), suggesting that attention may flow automatically across the representation of an object (Chen & Cave, 2006; Hollingsworth, Maxcey-Richard, & Vecera, 2012). These data are in accord with the notion that attentional facilitation, rather than being a spotlight that enhances the signal of perceptual representations in a uniform manner, instead interfaces with the neural architecture that forms those percepts and is thus informed by them (McMains & Kastner, 2011; Qiu et al., 2007; Scalf & Beck, 2010).

Visual attention also operates by inhibiting distracting information that conflicts with task performance. The efficacy of distractor inhibition is behaviorally indexed by measuring the influence of nontarget items on target responses. To the extent that such material impairs target responses, distractor inhibition is thought to have failed; to the extent that target responses are spared, distractor inhibition is thought to be successful. Although there has been some debate over whether distractor inhibition is simply an emergent property of attention-related enhancement (i.e., distractors are inhibited only relative to target material that was enhanced by attention), recent data indicate that distractor inhibition is indeed an active process that is independent from attentional enhancement (Gaspar & McDonald, 2014; Moher, Lakshmanan, Egeth, & Ewen, 2014; M. Suzuki & Gottlieb, 2013; for a review, see Geng, 2014). Like attentional enhancement, distractor inhibition can be applied in a top-down, proactive manner in advance of stimulus onset (Moher et al., 2014; Munneke, van der Stigchel, & Theeuwes, 2008) or may be reactively applied to specific stimuli (Dux & Marois, 2008; Suzuki &

Gottlieb, 2013). It reduces both the baseline (Ruff & Driver, 2006) and evoked (Gazzaley et al., 2007) activity of extrastriate cells whose receptive fields include the distracting information. The most recent data suggest that these reductions are observed very early in processing; an event-related potential component that indexes distractor suppression (i.e., the distractor positivity, or Dp) occurs within 250 ms of the onset of distracting material (Hickey, Di Loll, & McDonald, 2009; Sawaki, Geng, & Luck, 2012). The earlier P1 component, which is typically believed to reflect an early feed forward sweep of visual processing, is also reduced when evoked by inhibited distractors (Moher et al., 2014). Together, these data suggest that distractor inhibition is an early, active process that is distinct from attentional facilitation.

The notion that distractor inhibition is an early, top-down process distinct from attentional facilitation is relatively recent. Many facets of distractor inhibition remain relatively unexplored. One of these is whether it interacts with specific organizational processes that support visual perception as attentional facilitation does. Here, we ask whether distractor suppression interfaces with the suppressive processes that support figure–ground segmentation. Figure–ground segmentation fundamentally relies not only on facilitative (e.g., Lamme, 1995) but also on suppressive neural activity. As mentioned previously, regions of the visual field are perceived as ground as a result of losing the competition for figural status (e.g., Grossberg, 1994; Kienker et al., 1986; Peterson & Skow, 2008). Neuroimaging research reveals that the BOLD activation, in striate and extrastriate regions representing the ground, is suppressed (Cacciamani, Scalf, & Peterson, 2015; Likova and Tyler, 2008). Critically, ground suppression is not a unitary phenomenon; instead the potential of the ground to compete for figural status determines both the neural response to (Cacciamani et al., 2015) and behavioral influence of ground information (e.g., Peterson & Skow, 2008; Salvagio, Cacciamani, & Peterson, 2012). Ground regions that suggest familiar objects are more heavily suppressed than those that suggest unfamiliar objects; they evoke less signal in V2 (Cacciamani et al., 2015), and visual stimuli contained within those regions are more difficult to process (Salvagio, Cacciamani, & Peterson, 2012). This suppression also inhibits the processing of information that is categorically related to the figure suggested by the ground side; objects whose basic level category matches that suggested by the outline of a previously suppressed ground are more difficult to identify than those whose basic level category does not match that suggested by a previous ground (Peterson & Kim, 2001; Peterson & Skow, 2008). These latter data indicate that ground suppression is a complex process that engages multiple levels of the visual system rather than being a simple operation performed on local visual

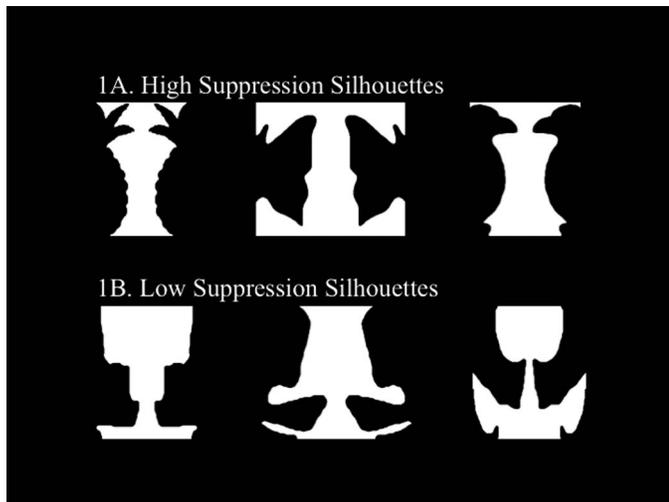


Figure 1. Silhouettes used in both Experiment 1 and Experiment 2. Silhouettes were biased so that the inside white region would be perceived as the figure and the outside would be perceived as the ground. All figures depicted novel objects. (A) Top row: High suppression silhouettes with portions of real-world, familiar objects suggested on the ground side of their left and right border. The suggested familiar objects are, from left to right: pineapples, butterflies, and eagles. Note that the familiar objects suggested on the grounds were not pointed out to the participants in our experiments. The participants were unaware of the familiar objects suggested on the ground side of the borders of the high-suppression silhouettes (see General Methods). (B) Bottom row: Low suppression silhouettes with portions of novel objects suggested on the ground side of their borders as well as the figure side. Silhouettes used in this task were reproduced with permission from Mary A. Peterson. The high suppression silhouette in the middle of the top row is reproduced from Figure 1 of Salvagio, E.M., Cacciamani, L., & Peterson, M. A. (2012). Competition-Strength-Dependent Ground Suppression in Figure-Ground Perception. *Attention, Perception, & Psychophysics*, 74(5), 964-978. Reproduced with permission of the author and the Psychonomic Society.

circuitry. We propose that these ground suppression mechanisms may interact synergistically with task-irrelevant distractor inhibition, such that distractors that fall on high-suppression grounds are more effectively inhibited than those that fall on low-suppression grounds. Such a finding would extend evidence that attention and perception modulate one another in a multiplicative manner (cf. S. Suzuki & Peterson, 2000) to include inhibitory processes.

General methods

To measure whether distractor inhibition operates more effectively when applied to stimuli that fall on

highly suppressed backgrounds, we used a variant of the Eriksen flanker task (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Eriksen & Eriksen, 1974) to index distractor inhibition. Participants indicated whether a central arrow pointed to the right or the left. Nontargets surrounded the central arrow. Nontargets were arrows pointing in the same direction (congruent), arrows pointing in the opposite direction (incongruent), or equal signs (neutral). Distractor interference was measured by comparing responses to incongruent trials with those to neutral trials. Facilitation was measured by comparing responses to congruent trials with those to neutral trials.

We examined whether differences in ground suppression altered distractor interference by manipulating whether or not a portion of a familiar object was suggested on the ground side of a silhouette figure. Familiarity is a strong cue for figural status; regions suggesting familiar objects are perceived as figures more often than matched regions suggesting unfamiliar objects (e.g., Peterson & Gibson, 1994; Peterson, Harvey & Weidenbacher, 1991). Familiarity is one of many figural cues, however; the figure is not necessarily perceived on the side of a border where a familiar object is suggested (Peterson, 1994). For instance, participants presented with small, bounded, enclosed silhouettes are likely to perceive the inside of the silhouette as the figure because many figural properties suggest it lies there. If the border implicitly suggests a familiar, real-world object on the ground side (see Figure 1A), the ground side is more suppressed than matched grounds of silhouettes with borders that do not suggest a familiar object on the ground side (see Figure 1B; e.g., Peterson & Skow, 2008; Salvagio et al., 2012). Consistent with this claim, the signal evoked in V2 and V4 regions representing the grounds of figures is reduced when a familiar object (see Figure 1A) rather than a meaningless shape (see Figure 1B) is implicitly suggested on the ground of a figure (Cacciamani et al., 2015). We exploit these stimuli to investigate whether distractor inhibition is specifically enhanced by ground suppression. Prior to the onset of the symbol display, participants were presented with silhouettes like those in Figure 1 that were enclosed, bounded, and symmetric. The vertical borders of half of the silhouettes suggested a portion of a familiar configuration—a meaningful real-world object on the outside/ground side (e.g., pineapples, as in the leftmost stimulus in Figure 1A). These were high-suppression ground silhouettes. The vertical borders of the other half of the silhouettes suggested novel, meaningless shapes on the outside (ground side) as well as on the inside (Figure 1B). These silhouettes were our control for low-level suppression; we expected that edge/feature units on opposite sides of their borders would compete, but that the associated suppression would be relatively low due to the lack of figure properties favoring that side as the

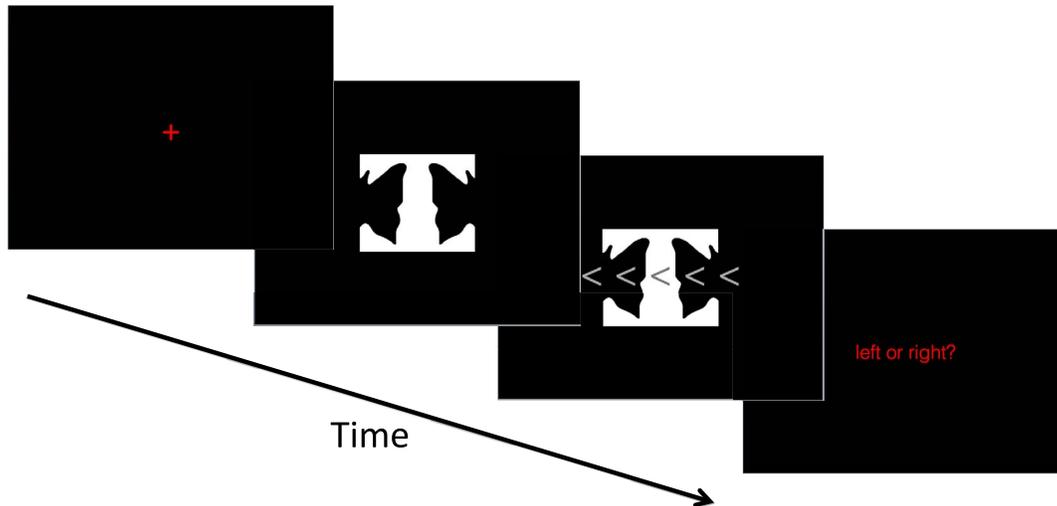


Figure 2. Flanker task Experiment 1. Participants were asked to respond to the right/left orientation of a central arrow. This example shows a congruent-style flanker task trial, where the central arrow is flanked by arrows pointing in the same direction, or congruently with it. The correct answer in this trial would be left. Silhouettes used in this task were reproduced with permission from Mary A. Peterson. Adapted from Figure 1 of Peterson, M. A., Cacciamani, L., Mojica, A.J., & Sanguinetti, J. L. (2012). The Ground Side of A Figure: Shapeless but not Meaningless. *Journal of Gestalt Theory*, 34 (3/4), 297-314. Reproduced with permission of the author and the Society for Gestalt Theory and its Applications.

object. These were low-suppression ground silhouettes. High and low suppression silhouettes were equated to the novel-object/novel-ground and novel-object/meaningful-ground silhouettes on the following low-level stimulus features: contour length, luminance, spatial frequency, and horizontal span (stimuli had the same vertical height) and on the figural properties of symmetry, area, and convexity (see Trujillo, Allen, Schnyer, & Peterson, 2010, for details).

The central arrow (i.e., the target) in the symbol display was superimposed on the silhouette figure; the nontargets were superimposed on the grounds (see Figure 2). Half of the nontargets fell on high-suppression grounds, and the other half fell on low-suppression grounds. We predicted that placing the nontarget items on high-suppression rather than low-suppression grounds would specifically reduce the negative behavioral consequences of incongruent nontargets and not the positive behavioral consequences of congruent nontargets. Such a finding would indicate that top-down distractor inhibition interacts with the suppressive perceptual mechanisms associated with figure-ground segmentation to improve task performance. Note that such an interaction can occur only after the incongruity between target and nontarget items has been detected; if the interaction between ground suppression and distractor inhibition were blind to the relationship among display elements, the influence of all nontarget items (both congruent and incongruent) on task performance should be reduced by high-suppression grounds.

Experiment 1

Methods

Participants

Seventy-eight undergraduate students at the University of Arizona participated in Experiment 1. All participants gave informed consent to participation. Participants were compensated with class credit. All participants reported having normal vision or corrected-to-normal vision.

Task and trial design

The trial design is shown in Figure 2. Participants began each trial by fixating on a red cross centered on a black backdrop. After 1000 ms, the cross was offset and a white silhouette was onset on a large black background. After a fixed stimulus onset asynchrony (SOA), a five-item row of gray symbols was superimposed on the silhouette and the background. The center item of this row was an arrow that pointed to the right or left; this was the target. The target appeared on the silhouette figure. The peripheral items were right-pointing arrows, left-pointing arrows, or equal signs; these were the distractors. The distractors appeared on the grounds. All display elements disappeared 100 ms after the onset of the symbols. Participants responded to the left/right orientation of the center symbol using the F and G keys on the computer keyboard with their left and right index fingers, respectively. We instructed

participants to respond to the central arrow as quickly and accurately as possible and to ignore any other stimuli presented throughout the experiment. Participants were given unlimited time to respond (M response time [RT] = 858 ms). RTs were recorded from the onset of the task-relevant symbols.

Previous behavioral experiments have observed that the ground suppression effect may vary with SOA (Peterson & Kim, 2001; Peterson & Skow, 2008; Salvagio et al., 2012). Evidence of more suppression of high-suppression than low-suppression grounds has reliably been obtained when task-relevant stimuli appear 80–100 ms after silhouette onset (Peterson & Kim, 2001; Peterson & Skow, 2008; Salvagio et al., 2012). Here, we presented symbol displays at SOAs of 50, 80, and 110 ms, in order to maximize the likelihood that we would observe ground suppression effects in at least one SOA. We randomly assigned participants to one of the three SOA conditions (25 participants were initially tested in the 50-ms condition, 25 in the 80-ms condition, and 28 in the 110-ms condition).

Stimuli

White silhouettes underlay the row of symbols. The inside of each silhouette was biased to be perceived as the figure by symmetry, enclosure, small area, fixation, and expectation. The silhouette figures all depicted novel objects. The silhouettes subtended 5° of visual angle vertically and ranged from 3.18° to 7.06° horizontally (at their widest point). The black screen backdrop was $44.3^\circ \times 24.8^\circ$. There were 66 silhouettes: 33 had portions of familiar objects suggested but not consciously perceived on the ground side (these were high-suppression ground silhouettes), and 33 had portions of novel shapes suggested on the ground side (these were low-suppression ground silhouettes). We administered a postexperiment questionnaire to ensure that the participants did not explicitly perceive the familiar objects suggested on the ground side.

The symbol displays consisted of one center arrow flanked by two nontarget symbols on each side. Items were separated by 0.1° of visual angle. They were medium gray (RGB = 0.5, 0.5, 0.5, range = 0–1). Nontarget symbols consisted of either arrows pointing in the same direction (congruent) or the opposite direction (incongruent) as the center target or equal signs, which indicated no direction (neutral). In Experiment 1, display elements were positioned such that the target element always fell on the figure, and nontarget elements (the flankers) always fell on the ground. Although the symbol display was always centered horizontally, its vertical position changed so that the target fell on the narrowest part of the figure and the flankers fell onto the ground (the center of the silhouette ranged 6° above and below fixation). Symbol

display elements also varied in height (range = 0.3° – 2°) and width (range = 0.5° – 3°) such that the center arrow extended almost to the ground-side border and the flankers fell only on the ground.

Experimental design

During the experiment participants viewed each silhouette once only; consequently, each participant performed 66 trials. Central stimuli were equally likely to point in each direction (33 trials each). Congruent, incongruent, and neutral flanking displays were equiprobable (22 trials per condition) and were equally likely to be superimposed over the high- and low-suppression grounds (11 trials per condition). Mapping of a given ground stimulus to a given flanker condition was random (except for the constraint that high- and low-suppression grounds were equally likely to appear in each flanker condition).

Postexperiment questionnaire: We asked all participants whether they saw any familiar objects on the outside of the figures. To aid participants' understanding of these questions, the experimenter showed an example of a high-suppression silhouette and pointed out the familiar object suggested on the ground side. The experimenter then asked if the participant had seen anything similar during the experiment. If participants gave any indication of seeing a familiar object on the ground side of a figure during task performance, their data were excluded from analysis (i.e., experimenters were instructed to write down a "yes" if the participant said "maybe" in response to this second question). It was necessary to eliminate these subjects because our experimental question required that the familiar objects suggested on the outside of the silhouettes lose the competition for figural status and be suppressed. In this case, subjects would not have been aware of them.

Equipment: Stimulus presentation and data collection were controlled using the Vision Egg (Straw, 2008). The experiment was performed on a Mac Mini Computer (Apple, Cupertino, CA) running OS X 10.8.4. The monitor was an Acer G205HV bd 20-in. class wide-screen LCD monitor with a screen resolution of 1600×900 , 16:9, 5000:1 dynamic (Acer, Inc., Xizhi, New Taipei City, Taiwan).

Results

We rejected data from participants who reported seeing something familiar on the ground side of the stimuli (assessed via verbal questioning; $n = 12$), whose average RTs were less than 100 ms ($n = 3$) from target onset (and thus likely reflected random responses), who deliberately responded to the flanking elements ($n = 3$; indicated by 91% error in the incongruent condition),

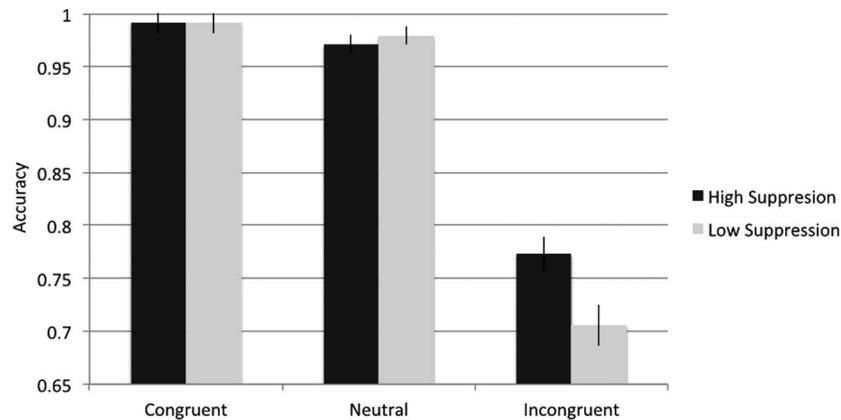


Figure 3. Experiment 1 results. Congruent trials were performed more accurately than neutral trials and incongruent trials. Neutral trials were performed more accurately than incongruent trials. Only incongruent trials showed an effect of ground suppression, such that the incongruent items were more successfully ignored if they fell on high-suppression grounds.

or whose accuracy across trials was more than 2.5 *SDs* below the mean ($n = 5$). This rejection procedure left $n = 19$ in the 50-ms SOA, $n = 17$ in the 80-ms SOA, and $n = 19$ in the 110-ms SOA condition.

Accuracy

We submitted arcsine square-root transformed accuracy data (means reported are back-transformed to accuracy) from 55 participants to a mixed measures ANOVA, using the within-participants factors of flanker consistency (congruent, neutral, and incongruent), ground suppression (high, low) and the between-participants factor of SOA (50, 80, 110 ms). We found a main effect of flanker congruency, $F(2, 104) = 111.08$, $p < 0.001$. Planned comparisons showed that accuracy was lower on incongruent flanker trials (74.0%) than on neutral flanker trials (97.5%; $t(54) = 11.07$, $p < 0.0001$) or congruent flanker trials (99.1%; $t(54) = 12.37$, $p < 0.0001$), and lower on neutral flanker trials than congruent flanker trials, $t(54) = 2.54$, $p = 0.021$. Thus, we observed typical flanker effects. The main effect was modified by an interaction between flanker congruency and ground suppression, $F(2, 104) = 4.183$, $p = 0.018$. As can be seen in Figure 3, high- and low-suppression grounds did not produce differential accuracy for trials with congruent (99.2% vs. 99.1%), $t(54) = 0.17$, $p = 0.87$, or neutral (97.1% vs. 97.9%), $t(54) = 0.83$, $p = 0.41$, flankers, but as predicted, if distractor inhibition interacts with ground suppression, high-suppression grounds reduced the negative influence of incongruent flanker items on target identification compared to low-suppression grounds. Performance on incongruent flanker trials was better when flankers appeared on high- versus low-suppression grounds (77.3% vs. 70.5%), $t(54) = 2.84$, $p = 0.006$. No other main effects or interactions approached conventional levels of significance ($p > 0.1$).

Response times

We submitted RT data from the same 55 participants to a mixed-measures ANOVA (Greenhouse-Geisser corrected), using the within-participants factors of flanker congruency (congruent, neutral, incongruent), ground suppression (high, low) and the between-participants factor of SOA (50, 80, 110 ms). We found a main effect of flanker congruency, $F(1.5, 78) = 21.80$, $p < 0.0005$. Planned comparisons showed that RTs were longer on trials with incongruent flankers (943 ms) than neutral flankers (836 ms), $t(54) = 4.03$, $p < 0.0005$, or congruent flankers (797 ms), $t(54) = 5.43$, $p < 0.0005$; and RTs were longer on trials with neutral flankers than congruent flankers, $t(54) = 2.52$, $p = 0.014$. No other main effects or interactions approached conventional levels of significance ($p > 0.1$). Critically, RTs were not longer for congruent flankers on the grounds of high-suppression silhouettes compared to low-suppression silhouettes; if anything they were faster although the differences are not significant ($p = 0.26$; see Table 1 for RT measures).

Discussion

We observed both interference from incongruent flankers and facilitation from congruent flankers, as is typical in flanker tasks. Critically, we found that the degree of suppression required to support figure–

Ground type	Congruent flankers	Neutral flankers	Incongruent flankers
High suppression	782 (67)	835 (84)	939 (85)
Low suppression	812 (79)	836 (70)	948 (84)

Table 1. Mean RTs in Experiment 1. Note: Standard errors are in parentheses.

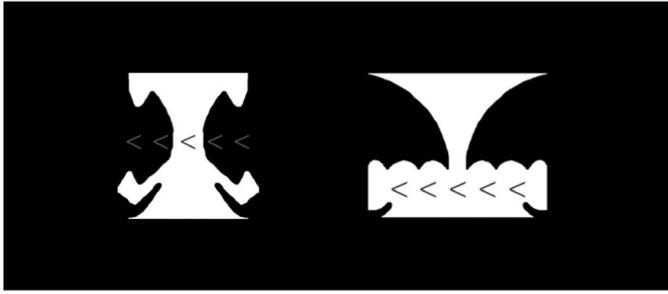


Figure 4. Flanker task Experiment 2. In Experiment 2, half of the trials displayed all four flanking items as well as the central target on the white figure (left). The remaining trials had only the central target on the figure and the four flanking items on the ground side of the figure/ground configuration (right), much like in Experiment 1. Silhouettes used in this task were reproduced with permission from Mary A. Peterson. The stimulus on the left was adapted from Figure 1 in Salvagio, E.M., Cacciamani, L., & Peterson, M. A. (2012). Competition-Strength-Dependent Ground Suppression in Figure-Ground Perception. *Attention, Perception, & Psychophysics*, 74(5), 964-978. Reproduced with permission of the author and the Psychonomic Society. The stimulus on the right was adapted from Figure 1 of Peterson, M. A., Cacciamani, L., Mojica, A.J., & Sanguinetti, J. L. (2012). The Ground Side of A Figure: Shapeless but not Meaningless. *Journal of Gestalt Theory*, 34 (3/4), 297-314. Reproduced with permission of the author and the Society for Gestalt Theory and its Applications.

ground segregation reduced interference from incongruent flankers, but not facilitation from congruent flankers. This supports the idea that inhibitory mechanisms of attention are amplified by suppressive mechanisms involved in figure-ground perception in a specific, multiplicative manner. Importantly, our finding that flanker facilitation was unaffected by the degree of ground suppression shows that, in our paradigm, ground suppression does not simply inhibit the representation of all nontarget items and thereby reduce their influence on behavior. Instead, processes specific to distractor inhibition are synergistic with perceptual suppressive mechanisms. One might be tempted to conclude that this interaction reflects a ceiling effect on flanker facilitation. Note, however, that we found a clear benefit of flanker consistency on both accuracy and RTs. We would expect this effect to be reduced if ground suppression simply reduced the influence of flanking information on performance in a uniform manner.

In Experiment 1, target items were located at the narrowest part of the figure. Participants' ability to locate this region during search may have been improved by their prior knowledge (albeit implicit) of the objects suggested by the ground-side borders of the high-suppression silhouettes. Prior experience with

visual information is well known to influence search patterns, even when participants are unaware of their familiarity with the search material (Ryan, Althoff, Whitlow, & Cohen, 2000). Implicit knowledge of the familiar ground sides might have facilitated search for the target, accounting for facilitated identification of targets with incongruent flankers for reasons unrelated to ground suppression. We address the viability of this alternative interpretation in Experiment 2.

Experiment 2

Methods

In this experiment, we altered the position of the symbol display items such that they fell entirely on the figure on 50% of the trials. On these trials, target items appeared at the widest point of the figure; they appeared at the narrowest point of the figure on all the remaining trials. This manipulation should have eliminated any search bias towards the narrowest part of the figures. It also allowed us to confirm that the effects we observed in Experiment 1 were caused by incongruent flankers falling into the suppressed ground regions of the silhouette rather than by a search set based on implicit access to representations of the familiar objects suggested on the ground side of high-suppression silhouettes. In Experiment 2, we anticipated that high-suppression grounds would selectively improve performance on incongruent trials only when the flanking elements fell on the ground of the display. If flanking elements fell on the figure of the display, we anticipated that there would be no difference between high- and low-suppression grounds for any trial type. Such a finding would indicate that distractor inhibition is amplified by the increased suppression of material falling on highly suppressed grounds rather than by any changes in search occasioned by ground-side familiarity.

All methods in Experiment 2 were identical to those used in Experiment 1, unless reported otherwise below.

Participants

A total of 69 undergraduate students at the University of Arizona participated in Experiment 2.

Experimental design

On 50% of the trials, flanking items fell on the ground of the silhouettes, as they did in Experiment 1. On the remaining 50% of trials, the flanking items fell on the figure (see Figure 4). Mapping of a given ground stimulus to a given flanker condition was random except for the constraint that high- and low-suppress-

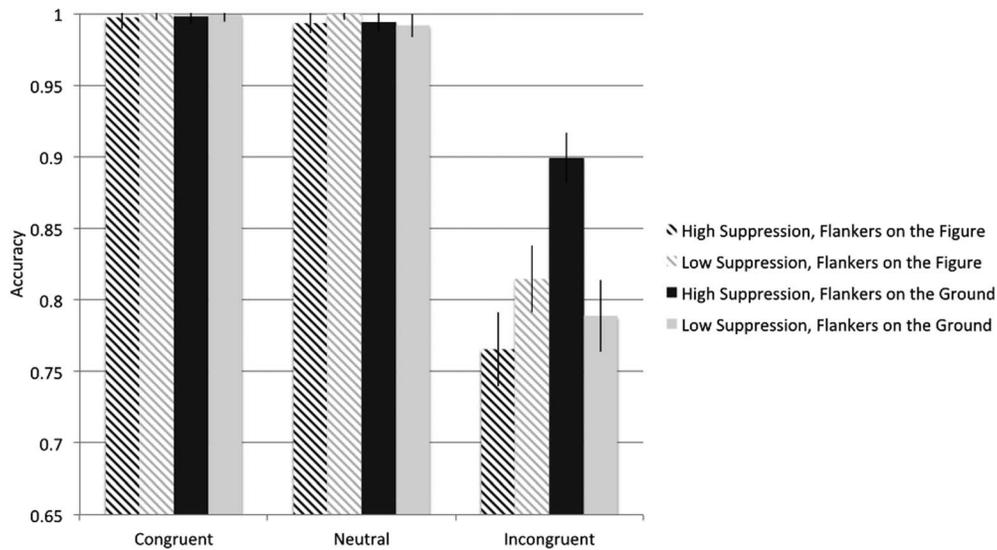


Figure 5. Experiment 2 results. Incongruent trials showed an effect of ground suppression only if flanking items fell on high-suppression grounds. Under these conditions, high-ground suppression promoted more successful target identification.

sion grounds were equally likely to be in each flanker condition. In an attempt to examine the longevity of ground suppression effects, we altered the SOAs between silhouette and target onset; these were 80, 100, and 140 ms (21 participants were initially tested in the 80-ms condition, 25 in the 110-ms condition, and 23 in the 140-ms condition). In other respects the design and procedure of Experiment 2 were identical to those of Experiment 1.

Results

We rejected data from participants who reported seeing something familiar on the ground side of the stimuli ($n = 8$), who responded with RTs < 100 ms ($n = 3$), or whose accuracy across trials was more than 2.5 SDs below the mean ($n = 1$). This rejection procedure left $n = 21$ in the 80-ms SOA, $n = 17$ in the 110-ms SOA, and $n = 19$ in the 140-ms SOA condition.

Accuracy

We submitted arcsine square-root transformed (means reported are back-transformed to accuracy) accuracy data from 57 participants to a mixed-measures ANOVA, using the within-subjects factors of flanker congruency (congruent, neutral, incongruent), ground suppression (high, low), flanker position (on the ground, on the figure), and the between-subjects factor of SOA (80, 110, 140 ms). Results are shown in Figure 5. We found a main effect of flanker congruency, $F(2, 108) = 180.44$, $p < 0.001$. Planned comparisons showed that accuracy was lower on trials with incongruent (82%) rather than neutral (99.5%, $t[56] = 9.97$, $p <$

0.0001) or congruent flankers (99.8%, $t[56] = 11.13$, $p < 0.0001$), and lower on trials with neutral rather than congruent flankers, $t(56) = 2.32$, $p = 0.024$). We found a three-way interaction among the factors flanker congruency, ground suppression, and flanker position, $F(2, 108) = 4.939$, $p = 0.009$. As predicted, incongruent flankers that appeared on high-suppression grounds had a smaller negative influence on accuracy (89.9%) than incongruent flankers in all other positions; on low-suppression grounds: 78.8%, $t(56) = 3.51$, $p = 0.0008$; on figures with high-suppression grounds: 76.5%, $t(56) = 4.36$, $p = < 0.0001$; and on figures with low-suppression grounds: 81.4%, $t(56) = 2.64$, $p = 0.01$. Neutral trials were best performed when flankers fell on the figures with low-suppression grounds (99.9%) rather than in other positions (on figures with high-suppression grounds: 99.3%, $t[56] = 2.17$, $p = 0.03$; on low-suppression grounds: 99.2%, $t[56] = 2.14$, $p = 0.04$; and on high-suppression grounds: 99.4%, $t[56] = 2.58$, $p = 0.01$). Ground condition did not differentially affect other trial types ($p > 0.2$). The three-way interaction encompassed significant two-way interactions between flanker position and ground suppression, $F(2, 108) = 12.3$, $p < 0.001$; flanker position and flanker congruency, $F(2, 108) = 5.805$, $p = 0.004$; and a marginally significant interaction between ground suppression and flanker congruency, $F(2, 108) = 2.364$, $p = 0.099$.

We also found a significant interaction between the factors of SOA and congruency, $F(4, 108) = 2.522$, $p = 0.045$. Planned comparisons showed that individuals exposed to the 110-ms SOA showed better performance with incongruent flankers (89.4%) than did those exposed to the 140-ms SOA (73.9%, $t[34] = 2.16$, $p = 0.04$). No other main effects or interactions were statistically significant ($p > 0.10$).

Flanker location	Ground type	Congruent flankers	Neutral flankers	Incongruent flankers
Off ground	High suppression	731 (30)	722 (19)	1028 (44)
	Low suppression	716 (21)	707 (19)	1120 (86)
On ground	High suppression	682 (22)	697 (17)	836 (30)
	Low suppression	697 (23)	720 (19)	882 (37)

Table 2. Mean RTs in Experiment 2. *Note:* Standard errors are in parentheses.

Previous work has shown that ground suppression effects may dissipate over time, such that none are in evidence in RTs to targets that appear 140 ms after exposure (Salvagio et al., 2012). This led us to present silhouettes and target stimuli with a range of SOAs (80, 110, 140 ms). We found no interaction between ground suppression and SOA. To be sure that ground suppression effects were indeed in evidence for the 140-ms condition, we submitted arcsine square-root transformed (means reported are back-transformed to accuracy) accuracy data from 19 participants to a mixed-measures ANOVA, using the within-subjects factors of flanker congruency (congruent, neutral, incongruent), ground suppression (high, low), and flanker position (on the ground, on the figure). We found a main effect of flanker congruency, $F(2, 36) = 56.191$, $p < 0.001$. Planned comparisons showed that accuracy was lower on trials with incongruent (74%) rather than neutral (99.7%, $t[18] = 7.72$, $p < 0.0001$) or congruent flankers (99.8%, $t[18] = 7.63$, $p < 0.0001$). We found a three-way interaction among the factors flanker congruency, ground suppression, and flanker position, $F(2, 36) = 4.501$, $p = 0.018$. As predicted, incongruent flankers that appeared on high-suppression grounds had a smaller negative influence on accuracy (84.1%) than incongruent flankers on low-suppression grounds (69.4%, $t[18] = 2.64$, $p = 0.02$) or on figures with high-suppression grounds (64.4%, $t[18] = 3.18$, $p = 0.005$). The three-way interaction encompassed a significant two-way interaction between flanker position and ground suppression, $F(2, 10.964) = 12.3$, $p < 0.004$.

Response times

We submitted RTs from 57 participants to mixed measures ANOVA (Greenhouse-Geisser corrected), using the within-subjects factors of flanker congruency (congruent, neutral, incongruent), suppression (high-ground suppression, low-ground suppression), flanker position (on the ground, on the figure), and the between-subjects factor of SOA (80, 110, 140 ms). We found a main effect of flanker congruency, $F(1.126, 60.8) = 47.57$, $p < 0.0005$. Planned comparisons showed that RTs were slower to trials with incongruent flankers (967 ms) than trials with neutral (711 ms, $p < 0.0005$) or congruent flankers (706 ms, $p < .0005$). Neutral and

congruent flankers did not produce significantly different RTs ($p = 0.62$). We found a main effect of flanker location, $F(1, 55) = 16.82$, $p < 0.0005$: RTs were faster when flankers were on the ground (748 ms) rather than on the figure (835 ms). Finally, we found a significant interaction between flanker location and congruency, $F(1.196, 64.44) = 10.30$, $p = 0.001$: Placing flankers on the ground had no effect on neutral trial RTs (flankers on the ground: 705 ms, flankers on the figure: 708 ms, $p = 0.67$); had a small, marginally significant effect on congruent trials (flankers on the ground: 689 ms, flankers on the figure: 723 ms, $p = 0.068$), and had a large, statistically significant effect on incongruent trials (flankers on the ground: 859 ms, flankers on the figure: 1073 ms, $p < 0.0005$). No other main effects or interactions approached conventional levels of significance ($p > 0.1$; see Table 2). Critically, RTs were not slower for congruent distractors shown on high-suppression grounds, as might be expected if ceiling effects on congruent trials prevented us from observing effects of ground suppression in the accuracy measure.

Discussion

In Experiment 2, we eliminated the possibility that the location of the flanker display, with respect to the figure, biased participants' search strategies toward one that might benefit from prior knowledge of the objects suggested on the ground side of high-suppression silhouettes. Because the target could appear on either the narrowest or widest part of the figure, participants could not have used knowledge of familiar objects in the high-suppression condition to guide their search towards the target location. We observed both interference from incongruent flankers and facilitation from congruent flankers across all trial types. For the trials in which flankers fell on the ground, we replicated the results of Experiment 1. Flanker interference was reduced when the flankers fell on high-suppression relative to low-suppression grounds, while flanker facilitation was unaffected by the degree of ground suppression. We did not observe these effects on trials in which the entire symbol display fell on the figure. This indicates that the synergy between distractor inhibition and ground suppression is specific to

conditions in which interfering material fell on the ground region. Consequently, these effects are likely driven by an interaction between distractor inhibition and local suppressive mechanisms that support figure-ground segmentation rather than some more general change in processing affected by variation in the degree of ground suppression.

We found that placing flanking items on the figure slowed responses for congruent and incongruent trials relative to neutral trials. These findings are not without precedent. Previous work shows that nontarget items that are identical to the target (rather than physically dissimilar to the target) can slow responses to a target item, particularly if the location of the target is not known in advance of stimulus onset (e.g., Bjork & Thomas, 1977), as in Experiment 2. Lateral interaction among similar stimuli has been suggested as one mechanism by which feature extraction may be impaired (e.g., Wolford & Hollingsworth, 1974). It is possible that flankers that fell on the figure (that is, the nonsuppressed region of the display) evoked stronger representations that were more likely to interact with each other in a mutually inhibitory manner. Alternatively, lateral inhibition might be enhanced for items that fall within the same surface of an object. Finally, items that fall on surfaces at different depths (as figure and ground do) are less likely to interfere with each other (Lehmkuhle & Fox, 1980). Future work might more directly investigate this issue.

As in Experiment 1, we observed no effect of SOA. Ground suppression lasted long enough to affect average accuracy when the SOA was as long as 140 ms. The ground suppression affected average RTs that were also longer (~830 ms) than those in tasks previously used (~580 ms). We thus extend the estimate of the longevity of ground suppression beyond that previously observed.

General discussion

We show that distractor inhibition interacts with the suppressive processes associated with determining that a region is a shapeless ground rather than a shaped figure. We examined performance in a variant of the Eriksen flanker paradigm. Consistent with previous research, we found that target identification accuracy was best when the nontarget items led to the same response as the target (congruent), intermediate when nontarget items were not an eligible response (neutral), and worst when the nontarget items led to a different response than the target (incongruent). The novel finding is that distracting, incongruent flankers (but not facilitative congruent flankers) influenced target identification less when they fell on the ground

side of high-suppression silhouettes rather than low-suppression silhouettes. We note that such results cannot be explained by a general mechanism that suppresses all information that falls onto high-suppression grounds; such a mechanism should have reduced both the facilitation from congruent flankers and the interference from incongruent flankers. The influence of ground suppression on the flanking items was unique to conditions in which flankers contained distracting, incongruent information that required inhibition.

Our findings indicate that distractor inhibition interacts with perceptual segregation processes such as ground suppression. They complement those demonstrating that attentional enhancement interacts with figure assignment (McMains & Kastner, 2011; Qiu et al., 2007). At first glance it might seem that our results could be caused by an interaction with attentional facilitation; that is, high-suppression grounds might improve performance by biasing facilitative attention towards the figure and the information contained within it. Previous work argues against this by demonstrating that the strength of ground suppression does not alter the ease with which attention is allocated to information inside the figure (Salvagio et al., 2012). The results of Experiment 2 also argue against this effect, as performance was not better in the on-figure condition for high-suppression rather than low-suppression silhouettes. Our data are better explained by a model in which task-dependent inhibitory mechanisms interact with those of ground suppression to reduce the influence of interfering nontarget information. They support an interface model of attention and perception, in which specific attentional mechanisms act on and interact with the neural systems that support visual perception (McMains & Kastner, 2011; Qiu et al., 2007; Scalf & Beck, 2010).

We observed interactions between the attentional status of the flanking items and the perceptual status of the grounds they fell upon only in the accuracy data. This is consistent with the notion that the level of ground suppression alters the action of distractor inhibition on percept formation, changes in the quality of which are especially likely to alter as task accuracy. This is because task accuracy improves when the perceptual data required to support the task (perceptual representation) improves, and declines when that data declines (e.g., Brehaut et al., 1999; Reinitz, 1990). Within the flanker task, congruence effects on accuracy are typically thought to reflect interference within perceptual processing stages (e.g., Santee & Egeth, 1982). When perceptual processing of flanking items is biased to be more extensive (by increasing the likelihood that flankers will be target congruent) their influence on target accuracy increases (Gratton et al., 1992). We suspect that in our paradigm, high levels of

ground suppression greatly increased the ability of top-down mechanisms to inhibit representation of incongruent flankers. This reduced the signal generated by those items and thus their ability to interfere with accurate identification of the target.

We observed that the level of ground-suppression influenced distractor suppression (the negative influence of incongruent flankers) but did not alter attentional facilitation (the positive influence of congruent flankers). This runs counter to the prediction of a simple push–pull attention mechanism in which attention to target information mandatorily inhibits distracting information (e.g., Pinsk, Doniger, & Kastner, 2004). If this were the case, attention to the central target letter should have automatically inhibited all flankers, at least to some degree, and this inhibition should have been amplified by ground suppression, reducing the influence of both facilitatory and distracting information. The specific influence of ground suppression on distracting information suggests that inhibition of the flankers was relatively independent of attention to the central target and that the baseline state of the visual system—that is, the extent to which information from the ground regions is suppressed—selectively determines the efficacy with which inhibition will be applied to distractors appearing in suppressed regions. This adds to a growing body of evidence that the inhibitory and facilitatory influences of selective attention on visual representations are separable, independent functions (e.g., Dux & Marois, 2008; Gaspar & McDonald, 2014; Moher et al., 2014).

Our results also inform our understanding of reactive inhibition; that is, inhibition that cannot occur until the distracting information has been identified as such. Our variant of the flanker paradigm required purely reactive inhibition in that participants could not know the locations, the features, or the size of distractor items in advance of their onset. Furthermore, flanking items required inhibition only if they were incongruent with the target, a decision that could not be made until both targets and distractors had been at least partially identified. Such distractor inhibition could of course not be applied early in the selective process; and indeed flanker interference is traditionally interpreted as evidence for late selection (e.g., C. W. Eriksen, Pan, & Botella, 1993) in that both the interference flankers generate and the resolution of it are believed to occur after perceptual processing has occurred. The alternative possibility is that flanker interference results from cross-talk among perceptual representations that impairs identification of the target; on this account, flanker interference must be resolved at an early stage—that is, during perceptual processing (e.g., Harms & Bundesen, 1983). Of course, these explanations both assume feed-forward, serial pro-

cessing of visual information and thus confound the time of processing (early, late) with the stage of processing (perception, response selection). Our findings speak strongly against such models (cf. Peterson & Cacciamani, 2013). We find that figure–ground segmentation, a basic perceptual operation that is irrelevant to the task, moderates a reactive inhibitory process that occurs only when a specific type of stimulus mismatch occurs (when target and flanking items lead to opposite responses). Thus, we have evidence that perceptual processing and attentional selection, rather than occurring serially, interact in a mutually informative manner to reduce the interference from task-irrelevant information.

Our results extend our understanding of the influence of ground suppression on target detection more generally. Although we find that ground suppression interacts with distractor inhibition, previous work has shown that it can also impair target enhancement if the target itself falls within the suppressed ground area (Salvagio et al., 2012). In the paradigm used by Salvagio et al. (2012) the discrimination task was difficult, attention to the targets on the grounds was required, and there were no nontarget items, either congruent or incongruent with the target (hence, reactive inhibition/facilitation did not play a role). Under these conditions, performance was worse for targets shown on high-suppression rather than low-suppression grounds, although it did not differ for other targets shown on the figure portion of silhouettes with high-suppression rather than low-suppression grounds. It remains for future work to further investigate the many ways in which ground suppression might interact with different mechanisms of attentional selection.

In summary, our findings support and extend models in which attentional function is actively informed by the functional neural architecture that supports visual perception (e.g., Franconeri et al., 2013; Robertson & Kim, 1999; Scaf et al., 2011; Scaf & Beck, 2010). The finding that distractor inhibition is uniquely informed by perceptual suppression adds to those demonstrating that attentional facilitation is influenced by object boundaries (e.g., Martinez et al., 2006; McMains & Kastner, 2011; Müller & Kleinschmidt, 2003; Qiu et al., 2007; Roelfsema, Lamme, & Spekreijse, 1998; Shomstein & Behrmann, 2006). That specific perceptual states give rise to unique interactions with individual selection mechanisms adds to the evidence that attention is informed not only by the availability and application of putative higher level resources to incoming information, but also by the visual mechanisms that support its representation.

Keywords: attention, figure–ground segregation, ground suppression, distractor inhibition

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