BRIEF REPORT

Feature-based attention is not confined by object boundaries: Spatially global enhancement of irrelevant features

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ABSTRACT

Theories of visual attention differ in what they identify as the core unit of selection. Feature-based theories emphasize basic visual features (e.g., color, motion), demonstrated through enhancement of attended features throughout the visual field, while object-based theories propose that attention enhances all features belonging to the same object. These theories make distinct predictions about the processing of features that are not attended primarily: Object-based theories predict that such secondary, task-irrelevant features are enhanced within object boundaries, while feature-based theories predict enhancement of irrelevant features across locations, regardless of objecthood. To test these two accounts, we had participants attend a set of colored dots among distractor dots (moving coherently upward or downward) to detect brief luminance decreases, while simultaneously detecting speed changes in other sets of dots in the opposite visual field. In the first experiment, we demonstrate that participants have higher speed detection rates in the dot array that matched the motion direction of the attended color array, although motion direction was task-irrelevant. In a second experiment, we manipulated the probability that speed changes occurred in the matching motion direction and found that enhancement of the irrelevant motion direction persisted even when it was detrimental for task performance, suggesting that spatially global effects of feature-based attention cannot easily be flexibly adjusted. Overall, these results indicate that features that are not primarily attended are enhanced globally, surpassing object boundaries.

Keywords Feature-based attention · Object-based attention · Visual attention · Perceptual grouping · Global feature enhancement

When confronted with a crowded visual scene, we can selectively process relevant information by attending to a particular feature (e.g., the color red) or object (e.g., a red car moving leftward; Carrasco, 2011; Desimone & Duncan, 1995; Maunsell & Treue, 2006). Different theories have advanced the importance of either basic visual features ("feature-based" attention) or bound objects ("object-based" attention) for non-spatial selection. These theories differ in what they consider to be the primary unit of attentional selection and propose different mechanisms for how such selection occurs.

Feature-based theories are primarily supported by the finding that attention to a feature at one location enhances processing of that feature throughout the visual field (Andersen et al., 2013; Martinez-Trujillo & Treue, 2004; Rossi & Paradiso, 1995; Sàenz et al., 2002; Wegener et al., 2008; White & Carrasco, 2011). For example, selection of the color red at one location enhances processing of that color across the visual field. Neural data indicates that enhancement of the attended feature occurs even at task-irrelevant locations (Andersen et al., 2013; Martinez-Trujillo & Treue, 2004; Sàenz et al., 2002; Treue & Martinez-Trujillo, 1999; Wannig et al., 2011), and even in the absence of visual stimulation (Serences & Boynton, 2007). This global effect of feature-based attention also has behavioral consequences, such as higher task performance when attending to the same feature in two locations than to opposing features (Andersen et al., 2008; Andersen et al., 2013; Sàenz et al., 2003; Störmer & Alvarez, 2014; Xiao et al., 2014). Similarly, attending to a specific feature in one task (a single direction of motion or orientation) can improve performance for matching features on a secondary task (White & Carrasco, 2011). Other results showed that a subthreshold motion prime improved participants' detection of the coherent motion *only* when the prime

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dots' color was the same as the color they attended elsewhere, suggesting that attending to a feature at one location can have secondary influences on perception of another feature at a different location through global enhancement of the attended feature (Melcher et al., 2005).

In contrast, object-based theories of attention state that objects are the core unit of attentional selection. Seminal studies on object-based attention showed advantages for shifting attention within an object (an outlined rectangle) relative to between objects (two outlined rectangles), even when the spatial distance between these attentional shifts was fixed (Egly, Driver, & Rafal, 1994), which was interpreted as attention spreading seemingly automatically within an object (Davis et al., 2000; Vecera & Farah, 1994). Later studies showed that this within-object spreading might depend on several factors, such as the spatial and configural uncertainty about the display, indicating that some of these object-based attention effects are likely dependent on task context and may be better explained with an attentional priority account, according to which under certain conditions attention prioritizes enhancement within objects (Chen & Cave, 2019; Shomstein & Yantis, 2002, 2004; Yeari & Goldsmith, 2010; for a recent review, see Shomstein, 2012). In all of these studies, however, object benefits are defined as enhanced processing within an object relative to between objects, assuming that object-benefits are confined—at least to some degree—by object boundaries (Baylis & Driver, 1993; Duncan, 1984; Scholl, 2001).[1]

Other studies of object-based attention have focused on investigating whether attention to one feature spreads to a "secondary" feature that is part of the same object. In particular, when objects have multiple features (e.g., an array of red dots moving upward), selecting one feature (e.g., the color red) can modulate processing of the second feature (e.g., upward motion). Evidence for this within-object spreading of attention comes from single-cell recordings in primates (Katzner et al., 2009), as well as human neuroimaging studies (Ernst et al., 2013; O'Craven et al., 1999; Schoenfeld et al., 2014; Schoenfeld et al., 2003). For example, it was found that hemodynamic responses related to the motion of an attended surface were increased even when participants were cued to attend to color, suggesting a spread of attention from the object's color to its motion direction (Ernst et al., 2013). In all of these studies, the primarily attended feature is cued initially, and participants are instructed to select that feature, while the secondary feature is considered task irrelevant, as participants are not cued to attend to it, nor is that secondary feature directly related to the task participants are performing. The fact that processing of the secondary feature is nonetheless

amplified solely through the voluntary selection of the primary feature has been taken as evidence for object-based theories of attention. Together, these results support a view in which all features of an object are efficiently and relatively automatically selected, while there are costs for selection beyond object boundaries (Duncan, 1984; Scholl, 2001).

Thus, theories of object-based and feature-based attention make distinct predictions about the processing of information that is not selected via top-down goals. According to a strict object-based view, attention should enhance processing of features that are part of the same object (but not between objects), while feature-based theories predict that features are enhanced across locations regardless of objecthood. That is, object-based theories imply that features of an object are attended *conjointly*, while feature-based theories imply that features are attended *independently*. The feature-based account has some initial empirical support from studies showing neural enhancement of unattended features at task-irrelevant location (Adamian et al., 2019; Bartsch et al., 2018; Boehler et al., 2011; Lustig & Beck, 2012); however, the perceptual consequences of this neurally assessed attentional spreading are not known, as these studies did not measure behavioral performance for the secondary, irrelevant features. Here, we examined how selecting a single feature of an object (i.e., its color) affects visual processing of a secondary feature of the same object (i.e., its motion direction) at another location. We find that processing of the secondary feature—that is part of the attended multi-feature object but never cued to be selected—is enhanced at another location. This processing benefit for the secondary feature persists even when it is detrimental for task performance, consistent with a relatively obligatory account of attentional spreading. We discuss these findings in the context of object-based and feature-based theories of attention, and argue that behavioral effects of attentional spreading within objects and across locations do not necessarily belong solely to one theory alone, as often suggested, but can provide important insights into the nature of attentional selection when considered together.

Experiment 1

In Experiment 1, participants monitored two dot-motion displays, one in each visual hemifield, and completed separate, independent tasks in each of them (see Fig. 1): a color selection task, in which they detected decreases in the luminance of dots in the attended color, and a motion task, in which they detected a speed increase in the other set of dots, regardless of motion direction. Here, we define objects as the spatially overlapping surfaces of dots in each visual field, as in previous research (e.g., Melcher et al., 2005; Schoenfeld et al., 2014; Schoenfeld et al., 2003; Katzner et al., 2009). Importantly, participants were only instructed to attend to one particular

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[1] Spreading of attention within an object has been shown to occur even when object boundaries are obscured or require perceptual completion (Behrmann et al., 1998; Davis & Driver, 1997; Moore et al., 1998) and for objects defined by shared surface properties (Adamian et al., 2019; Ernst et al., 2012).
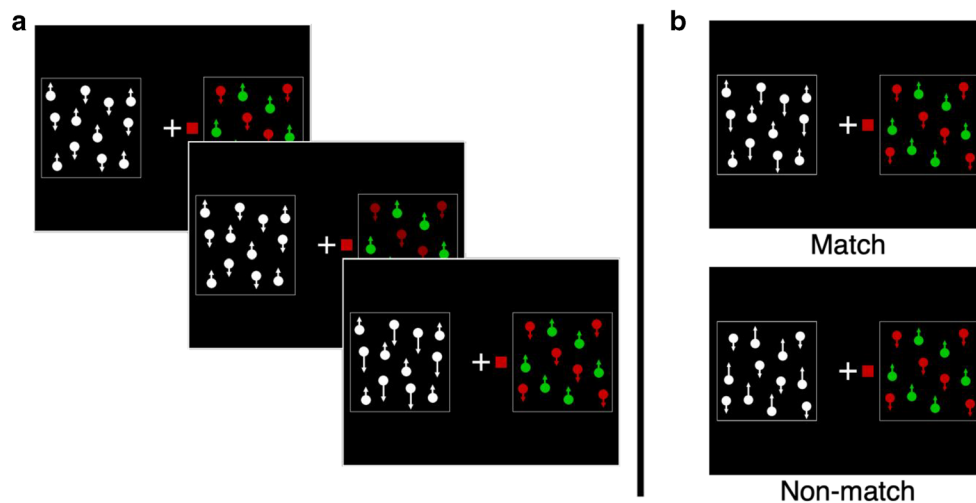
Fig. 1 Example of behavioral task. **a** Participants attended two displays, each containing two sets of dots moving in opposite directions (as indicated by the arrows, which were not present on the display in the experiment; also note that the dots are larger and fewer than in the actual experiment, and a box depicting the border of each dot display is included for illustration purposes). On each trial, a colored square in the center indicated which color of dots to attend to on that side of the display (in this example, attend red) to detect a brief decrease in the dots' color (amongst another), and although the dots were moving in two distinct directions, the direction of motion was irrelevant to the task. Thus, a particular color was cued at the beginning of each trial, and can thus be considered the primarily attended feature, while motion direction was never cued or mentioned to participants as a relevant feature, and thus served as a secondary feature of the object. For the motion task, participants were instructed to attend to all of the dots, regardless of their motion direction, to detect a speed increase. The speed increase could occur with the same probability in the dots moving in the same direction as those in the attended color (feature "match" trials), or in the opposite direction (feature "nonmatch" trials). Thus, attending to one particular motion direction was not helpful to perform well in this task. If attention to a particular color spreads to the motion direction of the same dot field and subsequently across the visual field, we expect that participants will better detect speed changes that happen to match the direction of the attended color than those that do not.

luminance (middle display). Simultaneously, participants were monitoring the noncolored (white) dots to detect a brief increase in speed (indicated by the longer arrows in the bottom display) of either set of white dots. **b** The main manipulation of interest concerned whether the speed change matched the direction of the attended color (top display, where both the speed change and the attended red dots were moving downward) or did not match (bottom display). (Color figure online)

Note that we obtained individual target detection thresholds prior to the experiment, but only while participants performed one of the two tasks at a time (see Procedure). Thus, it seems as if those five participants with poor performance had overall difficulties in dividing attention between the two tasks in the main experiment. The final sample ($n = 15$, 14 women) were 18–28 years of age ($M = 20.9 \pm 2.6$ years). This sample size provides 80% power to detect an effect of $d_z > 0.778$, smaller than previously reported for behavioral effects of feature-based attention (Sàenz et al., 2003; White & Carrasco, 2011). All participants provided written informed consent in accordance with the Institutional Review Board at UC San Diego.

Method

Participants

Twenty undergraduate students (18 women) from the University of California, San Diego, subject pool participated for course credit. Data from five participants whose performance on one of the tasks was extremely low were excluded from the main analysis ($d' < 0.5$ across all conditions in one task; in Experiment 2, we preregistered this exclusion criteria).

Stimuli

Participants were seated with a viewing distance of approximately 57 cm from the display. Two overlapping fields of dots ($9.0° \times 9.0°$ visual angle) were presented on a black background and centered $6.02°$ either side of fixation. One comprised two sets of colorful dots (red and green), the other comprised white dots. Each dot field contained 200 dots (each ~$0.2°$ diameter) moving either upward or downward at $2.25°/s$. To prevent observers from tracking single dots, each dot had a limited lifetime and was redrawn at a new random location every 300 ms.

In one of the dot displays, half of the dots were green [RGB: 20, 200, 20; luminance: 37.6 cd/m^2], and the remaining half were red [RGB: 200, 20, 20; luminance: 12.5 cd/m^2], and each set of colored dots moved either upward or downward (i.e., 100% overlap between color and motion direction thus comprising a dual-feature object). At the beginning of each

trial, participants were cued to attend to one of the colors (red or green) with a small color cue (a square in the color of the to-be-attended dots, 0.4° × 0.4°). This cue was presented slightly to the left or right of fixation (by 0.4°), indicating the side of the display that the colored dots would be presented (see Fig. 1). The color cue remained on the screen throughout each trial. After 800 ms, the two dot displays appeared and remained on the screen for 2 s. Dots in the attended color were always drawn on the display first and were occluded by the unattended colored dots if they overlapped. Participants were instructed to attend to the dots in the cued color to detect a brief luminance decrement (300 ms). At the end of each trial, participants had to indicate whether or not this change occurred in the attended dots. The change could occur in the attended dots (50% of trials), the unattended dots (25%), or neither set of dots (25%). The magnitude of the luminance decrement was determined for each participant using an independent thresholding task (see Procedure).

In the other dot display, all of the dots were presented in the same color (white [RGB: 200, 200, 200]); half of the dots moved upward, and the remaining half of the dots moved downward. Participants were instructed to identify a brief speed increase (300 ms) that occurred on half of the trials, and could occur in either motion direction. Importantly, half of the time the speed change occurred in the group of dots that were moving in the *same* direction as the attended colored dots presented in the other visual half-field (hereafter referred to as "match" trials), and the remaining half of the time the speed change occurred in the dots moving the *opposite* direction as the attended colored dots (hereafter referred to as "nonmatch" trials). Just like the luminance change, the magnitude of the speed change was determined individually for each participant using a thresholding task prior to the main task. The luminance and speed events were determined randomly and independently in each dot display. Each event lasted 300 ms and occurred randomly within one of three time windows (300–700 ms; 800–1,200 ms; or 1,300–1,700 ms after stimulus onset). If both events occurred on the same trial, they could not occur in the same time window and it was determined randomly which one occurred first.

Procedure

Participants first completed separate thresholding tasks for the color and the motion task to adjust task difficulty. During the thresholding procedure, participants were shown the same displays with two groups of overlapping dots presented left and right of fixation (see Stimuli), but were instructed to either only focus on the color task or the motion task. During the color thresholding, no speed changes occurred, and vice versa. The magnitudes of the luminance decrement (color task) and speed increase (motion task) were varied using a staircase procedure such that the change became smaller (less detectable) after two

consecutive hits, and larger (more detectable) after a miss. For the color task, the luminance decrement was initially set at 40% of the maximum luminance and was adjusted additively by 2% each step. For the motion task, the speed increase was initially set at 1.9× the base speed and was adjusted by 0.04 at each step. Participants completed 64 trials of each task separately (32 target events; the color thresholding was always completed first). Hit rates were fit with a logistic curve (guess rate = 0%) using the Palamedes toolbox (Prins & Kingdom, 2009), and thresholds were selected as the magnitude corresponding to 80% (color task) or 70% (motion task) hit rate. One participant completed the color thresholding twice, and two participants completed the motion thresholding twice, as performance was not fit well after one run.

In the main task (see Fig. 1), participants performed the color and motion tasks simultaneously. In particular, they were instructed to attend to the cued colored dots in one of the dot displays (e.g., in the right visual half-field) to detect luminance decrements in the attended color, and at the same time monitor for speed increases in the noncolored (i.e., white) dot display (e.g., in the left visual half-field). A speed increase occurred on half of the trials. Critically, participants were instructed to detect *any* speed increase, regardless of the motion direction of the dots (upward or downward). Note that this response format does not allow us to calculate false alarms in addition to hit rates, because participants reported only if they detected a change in speed, not its direction. This ensured that motion direction remained irrelevant for the motion task. At the end of each trial, participants were prompted to first indicate whether they saw a luminance decrement of the attended colored dots by pressing one of two keys on the keyboard ("m" for a detected change, "n" for no change) and were then asked to indicate whether they saw a speed increase of the noncolored (white) dots using the same keys. Participants completed 256 trials, which consisted of two full counterbalances of display side (color task left or right of fixation), attended color (green, red), color direction (upward, downward), luminance change (50% attended color, 25% unattended color, 25% no change), speed change (50% present, 50% absent), and speed change direction (upward, downward; also determines match or nonmatch trials). Thus, for both tasks the correct response was "change" on half of the trials. Match and nonmatch trials occurred equally often, and all trial types were randomly intermixed. Note that participants were always trained and thresholded on the color task before the motion task. In the main task, they also responded to events in the colored dots first. This procedure ensured that both tasks were treated as independent.

Results

Average accuracy was within the expected range on both the color task ($M = 73.4\%$, $SD = 7.9$) and the motion task ($M =$

74.7%, SD = 7.2), and did not differ across the two tasks, $t(14)$ = 0.53, p = .606, d_z = 0.14. Average hit and false alarm rates for each task are presented in the Supplementary Materials.

The main question of interest was whether the detection of speed increases in the motion task was influenced by which groups of dots were attended in the color task. We found that participants detected more speed changes in the group of dots that matched the motion direction of the attended color (M = 67.2%) than in the dots that did not match the attended color (M = 55.7%; Fig. 2), $t(14)$ = 5.89, p < .001, d_z = 1.52.[2] This indicates that when participants selected the color of the cued dots, attention not only enhanced visual processing of the primarily attended feature (color) but also processing of the overlapping secondary feature (motion direction); critically, this enhancement of the secondary feature was not confined to the attended group of colored dots, but instead propagated across the visual field and also enhanced processing of motion direction of the other noncolored dot group. This suggests that selecting a single feature can facilitate processing of secondary features that belong to the same object across the visual field.

Experiment 2

In Experiment 2 we tested whether the global spreading of attention to a secondary feature is sensitive to how beneficial or detrimental it is for task performance. In Experiment 1, enhanced processing of the motion direction of the colored dots (in addition to their color) may enable better performance in the color task, by decreasing the similarity between targets and distractors (Duncan & Humphreys, 1989; McLeod et al., 1988; Wolfe et al., 1989). However, attention to motion direction is not advantageous for the motion task because the speed change occurs equally often in each direction. There are two explanations for spreading of attention in this context: (1) spreading (within and between objects) is obligatory and occurs regardless of perceptual or task demands, or (2) the spread of attention is flexible and can be adjusted to exploit situations when it is advantageous or avoided when it is disadvantageous.

To test this, we manipulated the frequency of trials in which the speed change matched the direction of the attended color. For half of the participants, 80% of the trials matched, encouraging an "attend to direction" strategy; for the other half of participants, 20% of the trials matched, such that a strategy of "ignore direction" (or even "attend to opposite direction") would be most beneficial. If the spread of feature-based attention can be flexibly controlled, the size of the effect (match minus nonmatch accuracy) should be greater when matches are more frequent and should decrease when matches are unlikely. On the other hand, if attentional

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[2] When the data from excluded participants were included, this effect was smaller, but still present, $t(19)$ = 3.76, p = .001, d_z = 0.84.
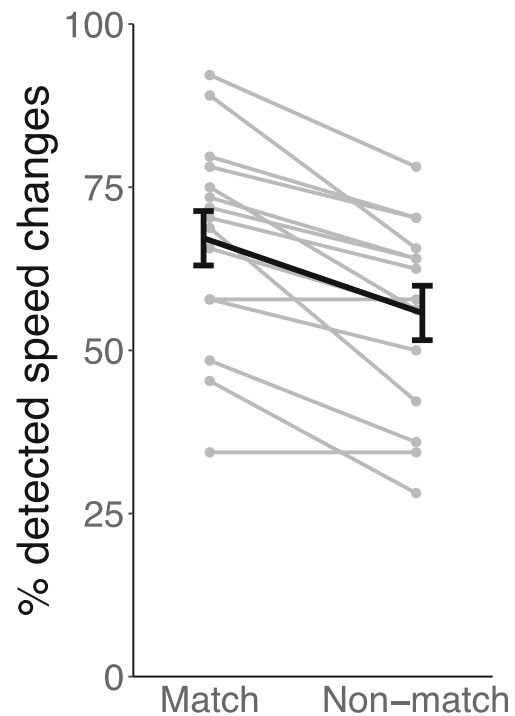

Fig. 2 Mean hit rates for speed change detection in Experiment 1. Gray points and lines correspond to individual participants, while the overlaid black line is the group mean with 95% within-subjects confidence intervals

spreading cannot be adjusted flexibly, the two groups should show an equivalent effect.

Method

Participants

This sample size provides 80% power to detect a difference between the groups of at least d_s > 0.83 (which corresponds approximately to a reduction in one group by 50% of the effect observed in Experiment 1). Fifty-six undergraduate students participated in Experiment 2 for course credit. Eight participants were excluded with d' < 0.5 across all conditions on one of the tasks. The remaining 48 participants (38 women) were randomly assigned to the high (80%) or low (20%) match condition. The final sample of participants were between 18–23 years of age (M = 20.0 ± 1.3 years) and had normal or corrected-to-normal vision.

Procedure

The procedure and stimulus details were identical to Experiment 1, with the exception that we manipulated the frequency of trials in which the speed change matched the

motion direction of the attended color. For half of the participants, 80% of the trials were match trials, encouraging an "attend to motion direction" strategy; for the other half of participants, 20% of the trials were match trials, such that a strategy of "ignore motion direction" (or even "attend to opposite direction") would be most beneficial. To avoid making motion direction explicitly task relevant, we did not instruct participants about this manipulation.

Participants completed 320 trials consisting of one full counterbalance of display side (color task left or right of fixation), attended color (green, red), color direction (upward, downward), luminance change (50% attended color, 25% unattended color, 25% no change), speed change (present, absent), and speed change direction (match to attended color, or nonmatch; 4-to-1 ratio dependent on condition). Just like in Experiment 1, participants' individual luminance and speed change thresholds were obtained prior to the main experiment. Out of the 48 participants included in the final analysis, 14 completed more than one run of thresholding before fits were acceptable (eight motion, five color, one both motion and color).

Results

The two groups did not differ in terms of their overall thresholds and performance, which we report in detail in the Supplementary Materials.

To assess whether participants could flexibly adjust the amount of spreading depending on the percentage of match/nonmatch trials, we conducted a 2 (trial type: match, nonmatch) × 2 (group: 20% or 80% matches) analysis of variance (ANOVA) on hit rates in the motion task. There was a main effect of trial type (match vs. nonmatch), $F(1, 46) = 18.21, p < .001, \eta_p^2 = 0.284$, replicating the main finding of Experiment 1 across the two groups on average. There was no main effect of group, $F(1, 46) = 0.38, p = .543, \eta_p^2 = 0.008$, and crucially no Group × Trial Type interaction, $F(1, 46) = 0.41, p = .527, \eta_p^2 = 0.009$, revealing that the two groups did not differ in detection rates of the speed changes on match and nonmatch trials (see Fig. 3). In each group, there was an advantage in detecting speed changes when they matched the direction of the attended colored dots ($M_{20\%} = 5.6\%$), $t(23) = 2.68, p = .014, d_z = 0.55$; ($M_{80\%} = 7.5\%$), $t(23) = 3.34, p = .003, d_z = 0.68$. Thus, even when the task was designed so that spreading of feature-based attention from color to motion direction would be more or less advantageous, the magnitude of the behavioral effect was unaffected.

Discussion

We assessed whether the enhancement of a secondary feature that overlaps spatially with an attended feature (and thus presumably belongs to the same object) results in spatially global facilitation of that feature. Participants performed a color-based selective attention task on a dot array on one side of the visual field, while at the same time monitoring for speed increases in separate dot arrays on the other side of the visual field.

Participants better detected speed changes in the dot array that matched the motion direction of the attended color array at the other location (i.e., opposite hemifield). Importantly, this was the case although motion direction was irrelevant to both tasks and never cued directly. We show that attentional enhancement of the secondary feature was not confined to the attended object, but that it was enhanced throughout the visual field.

How is processing of the secondary feature (motion direction) enhanced, given that participants were never cued to directly select it? Presumably, enhancement of the cued feature (color) occurred quickly and in a directed or voluntary manner, and only subsequently spread to the secondary feature (motion direction), likely in an incidental way, as many previous studies have shown (Ernst et al., 2013; O'Craven et al., 1999; Schoenfeld et al., 2014; Schoenfeld et al., 2003). One general concern that pertains to all studies using this sort of design to investigate attentional spreading to a secondary feature is that, in principle, participants could attend to the secondary feature—in our case motion direction—voluntarily. We think this is unlikely for several reasons. First, the color cue appeared prior to the onset of the dot array, enabling participants to bias visual processing towards the target color in advance. In contrast, motion direction was randomly assigned to one of the colors on a trial-by-trial basis, and so participants were not able to select the relevant motion direction before the trial began, so color selection had to precede motion selection. Second, participants were asked to detect a change in dots closely related to color (luminance decrement), rather than motion. Third, the target speed change in the secondary task could occur in either motion direction (Experiment 1) or even more often in the opposite motion direction (Experiment 2), discouraging participants from paying attention to motion direction. Thus, we believe that our task design allows a distinction in how the processing of color and motion direction was enhanced.

Our findings are broadly consistent with studies demonstrating that feature-based attention increases neural responses to features at irrelevant locations (Bartsch et al., 2018; Boehler et al., 2011; Katzner et al., 2009; Lustig & Beck, 2012), and behavioral studies reporting that aftereffects (Arman et al., 2006; Liu & Hou, 2011; Sohn et al., 2005) and priming (Melcher et al., 2005) are affected by feature-based attentional spreading. Here, we demonstrate that even when a feature is never cued to be selected, but is part of a multifeature object that comprises an attended feature, attention spreads to the secondary feature across the visual field, seemingly crossing
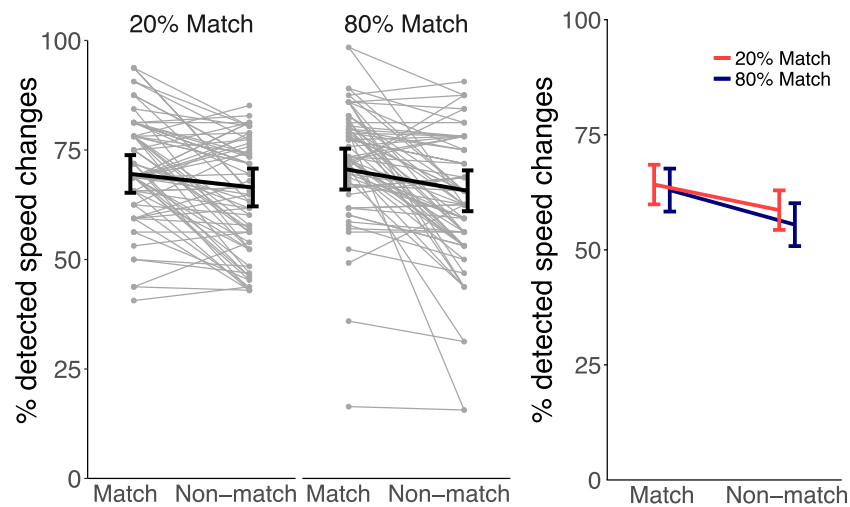
Fig. 3 Mean hit rate for speed changes in Experiment 2. In the left panel, gray points and lines correspond to individual participants, while the overlaid black line is the group mean. In the right panel, group means are plotted separately. Error bars are 95% within-subjects confidence intervals for each condition

object boundaries. Our findings suggest that attention is not confined to the attended object as often discussed in the literature on object-based attention (Adamian et al., 2019; Boehler et al., 2013; Egly et al., 1994; Lustig & Beck, 2012; Scholl, 2001), but instead spreads throughout feature maps, regardless of what objects these features belong to. These findings can be understood as a combination of object-based (i.e., within-object) and feature-based (i.e., across-object) spreading of attention. However, we believe that feature-based theories alone may be able to explain these effects. For example, consistent with the "feature-similarity gain hypothesis" (Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006; Treue & Martinez-Trujillo, 1999), neurons tuned to an irrelevant feature might be enhanced as a result of their shared spatial receptive field with the attended, currently behaviorally relevant feature. Specifically, at a local scale, the attended colored dots overlapped spatially with one particular motion direction (e.g., upward motion) in our tasks. Thus, it could be the case that the attended feature (color) is linked with the task-irrelevant feature (motion direction) through these small shared receptive fields. Under this framework, the spreading of attention from one feature to the other could be accounted for by attention at the level of independent features, with no additional assumptions about objects needed (Schoenfeld et al., 2014). Of course, such enhancement would not necessarily occur for every overlapping feature; attentional prioritization, for example, likely limits the spreading of attention between features (i.e., spreading would not occur from the unattended color to its concurrent motion direction). However, behaviorally, we cannot separate attention to each distinct feature, and so further evidence, assessing attentional modulation of multiple features independently (e.g., electrophysiological recordings; Andersen et al., 2015; Bartsch et al., 2018; Painter et al., 2014; Störmer & Alvarez, 2014) is necessary to test this hypothesis.

Such studies using neural measures could also test whether attentional spreading across separate objects occurs when the second object (e.g., white moving dots) is entirely task irrelevant and participants do not attend to it at all.

The present finding raises important questions about how this spreading is modulated by other task factors, such as the perceptual similarity between dot fields, perceived objecthood, or top-down control. Both feature-based (Martinez-Trujillo & Treue, 2004) and object-based (Shomstein & Berhmann, 2008) selection are known to be modulated by the similarity across features/objects, but it is an open question whether this spreading occurs across all shared features or only those that have some form of perceptual grouping (e.g., common fate through motion). However, because attentional spreading relies on different sets of objects with shared features, grouping by similar features likely contributes to the overall effect. This explanation would predict that the size of the observed effect should decrease as the number of shared features between different objects decreases (if the dots in the two tasks were different shapes; e.g., circles and triangles), the extent of which will be important for understanding the nature of attentional spreading in real-world situations. Additionally, such manipulations may provide further insights into the relationship between perceptual grouping, and feature-based and object-based attentional selection. Furthermore, apparent objecthood may potentially limit the extent of location spreading. In our task, objects were separated spatially, but other studies have used boundary boxes to manipulate perceived objecthood (e.g., Egly et al., 1994). Interestingly, feature spreading of directly attended features appears to occur robustly regardless of such boundary boxes (Xiao et al., 2014), in general agreement with the dominance of feature-based attentional spreading. Finally, while we show that attentional spreading persists even when it is detrimental

to task performance (Experiment 2), consistent with an obligatory account of attentional spreading, it could still be the case that in other task contexts participants can exert some control over the spreading to other locations (for example, if informed verbally about the probabilities). This would be an interesting future study to inform the debate on object-based and feature-based attention, as many feature-based studies have claimed obligatory spreading across locations (Andersen et al., 2013; Serences & Boynton, 2007), while spreading of attention within an object has been argued to be under some strategic control (Shomstein, 2012).

Overall, our findings suggest that attentional enhancement is not confined to features belonging to the same object, but can spread to features at another location. This suggests that attention is not confined by objecthood, but that features play an important role in selection independently of the objects they constitute. Critically, these features do not need to be attended primarily, but can simply "tag along" an attended feature (by being part of the same object or perceptual group) to receive a global boost in visual processing. Such spreading of feature-based attention to currently task-irrelevant features may increase sensitivity to features that will potentially become relevant in the near future.

References

Adamian, N., Andersen, S. K., & Hillyard, S. A. (2019). Parallel attentional facilitation of features and objects in early visual cortex. *Psychophysiology, 57*(3), Article e13498. https://doi.org/10.1111/psyp.13498

Andersen, S. K., Hillyard, S. A., & Müller, M. M. (2008). Attention facilitates multiple stimulus features in parallel in human visual cortex. *Current Biology, 18*(13), 1006–1009. https://doi.org/10.1016/j.cub.2008.06.030

Andersen, S. K., Hillyard, S. A., & Müller, M. M. (2013). Global facilitation of attended features is obligatory and restricts divided attention. *Journal of Neuroscience, 33*(46), 18200–18207. https://doi.org/10.1523/JNEUROSCI.1913-13.2013

Andersen, S. K., Müller, M. M., & Hillyard, S. A. (2015). Attentional selection of feature conjunctions is accomplished by parallel and independent selection of single features. *The Journal of Neuroscience, 35*(27), 9912–9919. https://doi.org/10.1523/JNEUROSCI.5268-14.2015

Arman, A. C., Ciaramitaro, V. M., & Boynton, G. M. (2006). Effects of feature-based attention on the motion aftereffect at remote locations. *Vision Research, 46*(18), 2968–2976. https://doi.org/10.1016/j.visres.2006.03.003

Bartsch, M. V., Donohue, S. E., Strumpf, H., Schoenfeld, M. A., & Hopf, J.-M. (2018). Enhanced spatial focusing increases feature-based selection in unattended locations. *Scientific Reports, 8*, Article 16132. https://doi.org/10.1038/s41598-018-34424-5

Baylis, G. C., & Driver, J. (1993). Visual attention and objects: Evidence for hierarchical coding of location. *Journal of Experimental Psychology: Human Perception and Performance, 19*(3), 451–470. https://doi.org/10.1037/0096-1523.19.3.451

Behrmann, M., Zemel, R. S., & Mozer, M. C. (1998). Object-based attention and occlusion: Evidence from normal participants and a computational model. *Journal of Experimental Psychology: Human Perception and Performance, 24*(4), 1011–1036. https://doi.org/10.1037/0096-1523.24.4.1011

Boehler, C. N., Schoenfeld, M. A., Heinze, H.-J., & Hopf, J.-M. (2011). Object-based selection of irrelevant features is not confined to the attended object. *Journal of Cognitive Neuroscience, 23*(9), 2231–2239. https://doi.org/10.1162/jocn.2010.21558

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research, 51*(13), 1484–1525. https://doi.org/10.1016/j.visres.2011.04.012

Chen, Z., & Cave, K. R. (2019). When is object-based attention not based on objects? *Journal of Experimental Psychology: Human Perception and Performance, 45*(8), 1062–1082. https://doi.org/10.1037/xhp0000657

Davis, G., & Driver, J. (1997). Spreading of visual attention to modally versus amodally completed regions. *Psychological Science, 8*(4), 275–281. https://doi.org/10.1111/j.1467-9280.1997.tb00438.x

Davis, G., Driver, J., Pavani, F., & Shepherd, A. (2000). Reappraising the apparent costs of attending to two separate visual objects. *Vision Research, 40*(10/12), 1323–1332. https://doi.org/10.1016/S0042-6989(99)00189-3

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193–222. https://doi.org/10.1146/annurev.ne.18.030195.001205

Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General, 113*(4), 501–517. https://doi.org/10.1037/0096-3445.113.4.501

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review, 96*(3), 433–458. https://doi.org/10.1037/0033-295X.96.3.433

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. https://doi.org/10.1037/0096-3445.123.2.161

Ernst, Z. R., Boynton, G. M., & Jazayeri, M. (2013). The spread of attention across features of a surface. *Journal of Neurophysiology, 110*(10), 2426–2439. https://doi.org/10.1152/jn.00828.2012

Ernst, Z. R., Palmer, J., & Boynton, G. M. (2012). Dividing attention between two transparent motion surfaces results in a failure of selective attention. *Journal of Vision, 12*(12):6, 1–17. https://doi.org/10.1167/12.12.6

Katzner, S., Busse, L., & Treue, S. (2009). Attention to the color of a moving stimulus modulates motion-signal processing in macaque area MT: Evidence for a unified attentional system. *Frontiers in Systems Neuroscience, 3*, Article 12. https://doi.org/10.3389/neuro.06.012.2009

Liu, T., & Hou, Y. (2011). Global feature-based attention to orientation. *Journal of Vision, 11*(10):8, 1–8. https://doi.org/10.1167/11.10.8

Lustig, A. G., & Beck, D. M. (2012). Task-relevant and task-irrelevant dimensions are modulated independently at a task-irrelevant location. *Journal of Cognitive Neuroscience*, 24(9), 1884–1895. https://doi.org/10.1162/jocn_a_00249

Martinez-Trujillo, J. C., & Treue, S. (2004). Feature-based attention increases the selectivity of population responses in primate visual cortex. *Current Biology*, 14(9), 744–751. https://doi.org/10.1016/j.cub.2004.04.028

Maunsell, J. H. R., & Treue, S. (2006). Feature-based attention in visual cortex. *Trends in Neurosciences*, 29(6), 317–322. https://doi.org/10.1016/j.tins.2006.04.001

McLeod, P., Driver, J., & Crisp, J. (1988). Visual search for a conjunction of movement and form is parallel. *Nature*, 332, 154–155. https://doi.org/10.1038/332154a0

Melcher, D., Papathomas, T. V., & Vidnyánszky, Z. (2005). Implicit attentional selection of bound visual features. *Neuron*, 46(5), 723–729. https://doi.org/10.1016/j.neuron.2005.04.023

Moore, C. M., Yantis, S., & Vaughan, B. (1998). Object-based visual selection: Evidence from perceptual completion. *Psychological Science*, 9(2), 104–110. https://doi.org/10.1111/1467-9280.00019

O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, 401, 584–587. https://doi.org/10.1038/44134

Painter, D. R., Dux, P. E., Travis, S. L., & Mattingley, J. B. (2014). Neural responses to target features outside a search array are enhanced during conjunction but not unique-feature search. *Journal of Neuroscience*, 34(9), 3390–3401. https://doi.org/10.1523/JNEUROSCI.3630-13.2014

Prins, N., & Kingdom, F. A. A. (2009). *Palamedes: Matlab routines for analyzing psychophysical data.* http://www.palamedestoolbox.org

Rossi, A. F., & Paradiso, M. A. (1995). Feature-specific effects of selective visual attention. *Vision Research, 35*(5), 621–634. https://doi.org/10.1016/0042-6989(94)00156-G

Sàenz, M., Buracas, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, 5(7), 631–632. https://doi.org/10.1038/nn876

Sàenz, M., Buracas, G. T., & Boynton, G. M. (2003). Global feature-based attention for motion and color. *Vision Research*, 43(6), 629–637. https://doi.org/10.1016/S0042-6989(02)00595-3

Schoenfeld, M. A., Hopf, J.-M., Merkel, C., Heinze, H.-J., & Hillyard, S. A. (2014). Object-based attention involves the sequential activation of feature-specific cortical modules. *Nature Neuroscience*, 17(4), 619–624. https://doi.org/10.1038/nn.3656

Schoenfeld, M. A., Tempelmann, C., Martinez, A., Hopf, J.-M., Sattler, C., Heinze, H.-J., & Hillyard, S. A. (2003). Dynamics of feature binding during object-selective attention. *Proceedings of the National Academy of Sciences*, 100(20), 11806–11811. https://doi.org/10.1073/pnas.1932820100

Scholl, B. J. (2001). Objects and attention: The state of the art. *Cognition*, 80, 1–46. https://doi.org/10.1016/S0010-0277(00)00152-9

Shomstein, S. (2012). Object-based attention: strategy versus automaticity. *Wiley Interdisciplinary Reviews: Cognitive Science*, 3(2), 163–169. https://doi.org/10.1002/wcs.1162

Shomstein, S. & Behrmann, M. (2008). Object-based attention: Strength of object representation and attentional guidance. *Perception & Psychophysics, 70*, 132–144. https://doi.org/10.3758/PP.70.1.132

Shomstein, S., & Yantis, S. (2002). Object-based attention: Sensory modulation or priority setting? *Perception & Psychophysics*, 64(1), 41-51. https://doi.org/10.3758/BF03194556

Shomstein, S., & Yantis, S. (2004). Configural and contextual prioritization in object-based attention. *Psychonomic Bulletin & Review*, 11(2), 247-253. https://doi.org/10.3758/BF03196566

Serences, J. T., & Boynton, G. M. (2007). Feature-based attentional modulations in the absence of direct visual stimulation. *Neuron*, 55(2), 301–312. https://doi.org/10.1016/j.neuron.2007.06.015

Sohn, W., Chong, S. C., Papathomas, T. V., & Vidnyánszky, Z. (2005). Cross-feature spread of global attentional modulation in human area MT+. *NeuroReport*, 16(12), 1389–1393. https://doi.org/10.1097/01.wnr.0000174059.57144.62

Störmer, V. S., & Alvarez, G. A. (2014). Feature-based attention elicits surround suppression in feature space. *Current Biology*, 24(17), 1985–1988. https://doi.org/10.1016/j.cub.2014.07.030

Treue, S., & Martinez-Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, 399, 575–579. https://doi.org/10.1038/21176

Vecera, S. P., & Farah, M. J. (1994). Does visual attention select objects or locations? *Journal of Experimental Psychology: General*, 123(2), 146–160. https://doi.org/10.1037/0096-3445.123.2.146

Wannig, A., Stanisor, L., & Roelfsema, P. R. (2011). Automatic spread of attentional response modulation along Gestalt criteria in primary visual cortex. *Nature Neuroscience*, 14(10), 1243–1244. https://doi.org/10.1038/nn.2910

Wegener, D., Ehn, F., Aurich, M. K., Galashan, F. O., & Kreiter, A. K. (2008). Feature-based attention and the suppression of nonrelevant object features. *Vision Research, 48*, 2696–2707. https://doi.org/10.1016/j.visres.2008.08.021

White, A. L., & Carrasco, M. (2011). Feature-based attention involuntarily and simultaneously improves visual performance across locations. *Journal of Vision*, 11(6), 1–10. https://doi.org/10.1167/11.6.15

Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 15(3), 419–433. https://doi.org/10.1037/0096-1523.15.3.419

Yeari, M., & Goldsmith, M. (2010). Is object-based attention mandatory? Strategic control over mode of attention. *Journal of Experimental Psychology: Human Perception and Performance*, 36(3), 565–579. https://doi.org/10.1037/a0016897

Xiao, G., Xu, G., Liu, X., Xu, J., Wang, F., Li, L., Itti, L., & Lu, J. (2014). Feature-based attention is independent of object appearance. *Journal of Vision, 14*(3), 1–11. https://doi.org/10.1167/14.1.3