Irrelevant digits affect feature-based attention depending on the overlap of neural circuits

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Accepted 13 July 2001

Abstract

Feature-based attention was investigated by examining the effect of irrelevant information on the processing of relevant information. In all experiments, irrelevant information consisted of digits whose semantic information is known to be processed in parietal areas. Between experiments we varied the degree of parietal involvement in the processing of the relevant feature. The influence of the irrelevant digit on the binary manual response task on the relevant feature was measured by the SNARC effect, a spatial numerical association of response codes demonstrating faster left than right hand responses for small numbers and faster right than left hand responses for large numbers. When processing of the relevant feature depended on parietal cortex, as is the case for orientation processing (exps. 1 and 4), there was an effect of the digit’s semantic value on response times. Conversely, there was no effect of the irrelevant digit on the processing of color (exps. 2 and 3) or shape (exp. 5), which rely only minimally on parietal resources. After ruling out alternative explanations we conclude that the efficiency of feature-based attention is determined by the degree of neural overlap of structures dedicated to process relevant and irrelevant information.

1. Introduction

Efficient behavior requires selection of information. In the domain of vision, the information acting upon our retinas is too abundant to be processed all to the same degree during the conversion of sensory input into goal-oriented behavioral output. Attentional mechanisms provide a means to give privilege to a subset of the available information [25,43]. Selection can be accomplished on the basis of a particular area in space [23,35], a certain object [14,44,46] or a particular visual feature [8,9,26]. In this paper we focus on feature-based attention.

Single-unit studies [29,41] and functional imaging studies [6,8,9,34] indicate that feature-based attention modulates visual processing in specific areas of neocortex depending on which feature is being attended. Thus feature-based attention operates as a localized neural adaptation to the task at hand. In line with this view, it is possible that the quality of feature-based selection depends on the extent to which relevant and irrelevant information are active in the same neural structures. That is to say, interference from irrelevant information on feature-based attention would be stronger if the relevant and the irrelevant feature are processed by the same neural structures than if both features pass through different neural structures.

To test this hypothesis, we devised a behavioral paradigm in which we varied the relevant information while keeping irrelevant information constant. As irrelevant information we used digits. Functional imaging (e.g. Refs. [7,33]), electrode recordings [1] and patient studies (e.g. Ref. [12]) convergently demonstrate the involvement of superior and inferior parietal areas in the semantic processing of the numerical magnitude of digits. The pre-semantic physical identity of digits is processed in
inferior extrastriate cortical areas [2,33]. Behavioral studies suggest that magnitude-related information is autonomously activated, as witnessed by effects of number magnitude on processing times in tasks for which a mere visual analysis of the digit suffices [10]. As relevant information we used either contour-based 2D shape, color, or orientation. These features are processed to a different degree by parietal areas. Parietal involvement in the processing of shape and color is very restricted, whereas it is more extensive in the case of orientation processing [15–17,19,32,37,38,45], not only in visually-guided motor tasks [30,32] but also in associative visuo-motor transformation tasks like the two-choice manual response task adopted here [17,19,37,38]. Accordingly, we expected that semantic interference from number would be observed with attention to orientation, but not or to a lesser degree with attention to color or shape.

Semantic processing of digits can be evaluated in a binary manual response task. Dehaene et al. [11] first showed an association between numerical value and the side of the response and labeled this effect the SNARC effect (spatial numerical association of response codes). Participants were asked to press one of two keys in response to an even number and the other key to an odd number. Smaller numbers were responded to faster with the left hand than with the right hand. The reverse happened for larger numbers. Additional control experiments confirmed that the SNARC effect originates from accessing a number’s semantic magnitude representation, which is conceived of as a position on a left-to-right oriented mental number line [4,11] such that there is congruity between small numbers and left-hand responses and between large numbers and right-hand responses. Therefore, we used the SNARC effect as a marker for semantic access. By having subjects direct attention away from the digit and asking them to perform a two-choice manual response task, we can evaluate the extent to which the unattended digit is processed as a function of the kind of processing being performed attentively.

2. Materials and methods

2.1. Participants

Sixty-eight Dutch-speaking subjects participated in the study. All participants had normal or corrected vision, and reported to be neuropsychologically healthy. Experiments 1–2 and 3–4 were each tested on the same sample (each 24 participants), in which case the order of experiments was counterbalanced. Subsamples were composed comparably in terms of age (exps. 1–2: 19.3; exps. 3–4: 18.3; exp. 5: 24.2), sex (number of male participants: exps. 1–2: 7; exps. 3–4: 4; exp 5: 11), handedness (number of right-handed participants: exps. 1–2: 20; exps. 3–4: 20; exp. 5: 16) and education (all participants were students or recent graduates in psychology).

2.2. Stimuli

The numbers used ranged from 0 to 9 (except exp. 5, 1 to 9) and were presented centrally on a black background as Arabic digits in Borland C’s simplex font (VGA card in graphics mode). The digit subtended an area of 18×38 mm. In the color the digit was colored in standard red or green (exp. 2) and light cyan and cyan (exp. 3), as standardly defined in Borland C’s library. In all other experiments the digits were presented in white with a visual stimulus superimposed in the centre. In exp. 1 this stimulus was a triangle pointing upward or downward (subtending 18×18 mm). In exp. 4 an oriented line segment (18×1 mm) was superimposed on the digit and in exp. 5 a circle or a square (18×18 mm).

2.3. Procedure

Participants had to press one of two response keys, depending on the relevant feature (exp. 1: triangle pointing upward or downward; exp. 2: red or green; exp. 3: light or dark cyan; exp. 4: horizontal or vertical line; exp. 5: circle or square). Key assignment was counterbalanced across participants. Before the actual experiment the participants took part in a training session, consisting of 20 trials with letters instead of numbers. In the training session an auditory feedback buzz was given when the participant pressed the wrong key. In the actual test session, each number was presented a fixed number of times (32 in exps. 1, 2 and 5; 24 in exps. 3 and 4); half of the times with the one relevant feature, the other half of the times with the other relevant feature. The whole set of trials was presented in randomized order with a different randomization for each subject.

Each trial started with the symbol ‘#’ as fixation point (18 mm×50 mm) presented at the center of the screen for 1000 ms. The subjects were asked to fixate this point, but eye position was not monitored. Thereafter, the screen was erased and immediately followed by the stimulus. The stimulus remained on until a response was made, which was registered to the nearest ms from stimulus onset. A blank screen followed for 500 ms, after which the next trial started. The two response buttons were connected to a PC-compatible Pentium computer, were placed at a comfortable position in front of the subject and were separated by ~30 cm. The eye–screen distance was plus or minus 70 cm. Both speed and accuracy were stressed in the instructions, and the interval of numbers used was explicitly mentioned.

2.4. Data analysis

Trials with an RT shorter than 150 ms or longer than 1000 ms were discarded from all analyses. The cut-off value of 1000 ms fell well outside the grand average plus three standard deviations. This way, less than 1.5% of the data are excluded.
The presence of a SNARC effect was evaluated by means of a regression analysis of repeated measures data as described by Lorch and Myers [28]. We reported the advantages of this analysis elsewhere [18]. In a first step, for each subject the median RT of the correct responses was computed for each number, separately for left and right responses. On the basis of these medians, differences in RT (dRTs) were computed by subtracting the median RT for the left hand from the median RT for the right hand. If there is an association between response side and number magnitude, we expect a negative correlation between number magnitude and dRT: relatively small numbers should elicit faster left responses, resulting in positive dRTs, whereas relatively large numbers should elicit faster right responses, and thus negative dRTs. Therefore, in a second step, a regression equation was computed per subject with number magnitude as predictor variable. In a third step t-tests were performed to test whether the regression weights of the group deviated significantly from zero. Since only a negative slope is expected theoretically, all reported P-values are one-tailed.

3. Results

3.1. Experiment 1: orientation, triangle pointing upwards or downwards

Participants had to determine the orientation of a triangle superimposed on a digit (ranging from 0 to 9). Participants had to indicate whether the triangle was pointing upwards or downwards. A triangle was chosen as task relevant feature because it is perceptually salient and can be easily segregated from the digit background, in terms of Gestalt laws on the basis of good continuation and closure. Lesions of inferior parietal cortex have been shown to impair the discrimination of rotated shapes in the monkey [15,45]. Single-cell recordings reported orientation selective cells in the anterior intraparietal area [32]. Functional brain imaging demonstrated the involvement of parietal areas in the processing of spatial features like orientation [16,17,19,37,38].

Error rate averaged over subjects was 3.0% (with a maximum of 6.1%). There was no speed–accuracy trade-off, as indicated by the absence of a negative correlation between RT and number of errors, computed over 20 data couples (10 numbers, separated for left and right responses), r = +0.30; n = 20; P < 0.30. Mean RTs of correct responses with the digits 0 to 9 as irrelevant information were, respectively, 453, 452, 457, 467, 468, 465, 454, 455, 445 and 460 ms.

The regression analysis of repeated measures data revealed the following equation (presented in Fig. 1):

dRT = −0.27 − 2.03 magnitude.

The significant contribution of number magnitude to the pattern of left hand–right hand differences (r(23) = −2.91, S.D. = 3.4, P < 0.005) reflects a reliable SNARC effect (with a negative slope observed in 17 participants) and shows that the unattended digits were processed semantically. As Brysbaert [4] has argued, the semantic coding of the number zero might be different than the semantic coding of other numbers. To make sure that this cannot bias our results, we also provide regression equations computed on the numbers 1 to 9. This reveals a nearly

![Exp. 1: Orientation: Triangle pointing up - down](image_url)

Fig. 1. Differences in RT (dRT) between right and left hand responses (right–left) as a function of the irrelevant digit. Squares indicate the observed dRTs. The continuous line depicts the predicted dRTs on the basis of the regression analysis.
identical result: \( dRT = -0.22 - 2.03 \) magnitude \( (t(23) = -2.03, P < 0.05) \).

The fact that there is a majority of negative dRTs does not obstruct the acceptance of a SNARC effect as it is highly likely that this is a result of the fact that a large majority of the participants was right-handed, resulting in overall faster right-hand responses. Then, the SNARC effect shows how this right-hand advantage is modulated by the magnitude of the presented number.

3.2. Experiment 2: color, red or green

In experiment 2 the relevant feature was changed to color. As parietal cortex is not involved in the processing of color [5,47] but relies primarily on structures in the ventral stream, less interference from the irrelevant digits is expected if participants respond to color as the relevant feature. In fact, luminance was not controlled. For the present purposes, however, the difference between color and luminance is unimportant as the neural correlates of attentive selection for color and luminance have been shown to be essentially the same [31].

Error rate averaged over subjects was 2.5% (with a maximum of 7.7%). There was no speed–accuracy trade-off, as indicated by the absence of a negative correlation between RT and number of errors, computed over 20 data couples (10 numbers, separated for left and right responses), \( r = -0.02; n = 20; P < 1 \). Mean RTs of correct responses with the digits 0 to 9 were, respectively, 385, 386, 385, 388, 376, 375, 386, 378 and 380 ms.

The following equation was obtained and is presented in Fig. 2:

\[ dRT = -12.8 + 0.5 \text{ magnitude.} \]

Magnitude was not reliably different from zero \( (t(23) = 0.44; \text{S.D.} = 6, P < 0.3, \text{with a negative slope in 10 participants}) \). Omission of zero from the regression analyses reveals a similar equation: \( dRT = -14.3 + 0.78 \text{ magnitude} \) \( (t(23) = 0.6; P < 0.25) \). The direct comparison of the magnitude slopes in experiments 1 and 2 revealed a reliably more negative slope in the orientation task than in the color task \( (t(23) = -1.86; P < 0.05) \). Thus, whereas a reliable SNARC effect was obtained when orientation was the relevant feature, the SNARC effect completely disappeared when subjects attended to color.

3.3. Experiment 3: color, light cyan and dark cyan

Average RTs in experiment 2 were considerably shorter than in the orientation task. Possibly, latencies were simply too short for the number semantic system to become sufficiently activated to affect performance in the color task. In order to evaluate this alternative interpretation, a new color/luminance discrimination experiment was carried out, using less discriminable colors/luminances (light and dark cyan).

Error rate averaged over subjects was 4.5% (with a maximum of 12.9%). There was no speed–accuracy trade-off, as indicated by the absence of a negative correlation between RT and number of errors, computed over 20 data couples (10 numbers, separated for left and right responses), \( r = 0.47, n = 20; P < 0.05 \). Mean RTs of correct responses with the digits 0 to 9 were, respectively, 499, 513, 505, 492, 494, 492, 481, 500, 489 and 489 ms.

![Exp. 2: Color: red - green](image-url)
Even when the colors were chosen such that the average latency was raised considerably (from 382 to 492 ms) up to a level at which a SNARC effect was obtained in experiment 1 (457 ms), there was no indication of an effect of semantic processing of the digit. The following equation was obtained and is presented in Fig. 3:

\[ dRT = -8.31 + 1.95 \text{ magnitude}. \]

Magnitude tended to be positive, the reverse of the SNARC effect, but was not reliably different from zero \((t(23)=1.5; \text{S.D.}=6.8; P<0.1, \text{with eight participants exhibiting a negative slope})\). The same was true for the regressions computed with zero excluded: \(dRT=-12.45+2.8 \text{ magnitude} \,(t(23)=1.58; P<0.1)\). Inspection of the dRTs for the individual numbers suggests a categorical effect of number magnitude. It has been shown that when precise numerical magnitude is irrelevant to the task, a stimulus can automatically be classified as small or large without coding the precise numerical value \([42]\). This crude small–large classification has been argued to be essentially different from refined numerical coding \([20,42]\). Further research is needed to test whether the tendency observed here is a systematic effect and, if so, to explain why crude magnitude information is associated with spatial coordinates of response codes, opposite to refined numerical magnitude.

### 3.4. Experiment 4: orientation, horizontal or vertical line segment

To enable a direct comparison of the results of experiment 3 with the same set of participants, the participants of experiment 3 were subjected to an orientation task with lines instead of triangles. The line could be either vertical or horizontal. An oriented line rather than a triangle was used as a target to evaluate generality.

Technical failure caused data loss for one participant. Error rate averaged over subjects was 3.5% (with a maximum of 13.3%). There was no speed–accuracy trade-off, as indicated by the absence of a negative correlation between RT and number of errors, computed over 20 data couples (10 numbers, separated for left and right responses), \(r=0.16; n=20; P<1\). Mean RTs of correct responses with the digits 0 to 9 were, respectively, 468, 491, 479, 475, 509, 471, 468, 485, 466 and 476 ms.

Regession equations were computed in order to test for the presence of a SNARC effect. The following equation was obtained and is presented in Fig. 4:

\[ dRT = -1.48 - 3.74 \text{ magnitude}. \]

Number magnitude was reliably activated, as witnessed by a significant SNARC effect \((t(22)=-3.59; \text{S.D.}=5.0; P<0.001 \text{ with a negative slope in 18 participants})\). Without zero, the equation was \(dRT=13.0-5.13 \text{ magnitude} \,(t(22)=-3.67; P<0.001)\). The direct comparison of the magnitude slopes from experiments 3 and 4 reveals a reliably more negative slope in the line orientation experiment \((t(22)=-3.27; P<0.01)\), whereas RTs between the two tasks did not differ \((t(22)=0.76; P<1)\).

### 3.5. Experiment 5: shape, circle or square

So far, the SNARC effect was present in those situations...
4. Discussion

In a series of experiments we showed that interference from irrelevant information on feature-based attention is stronger if the relevant feature is processed by the same neural structures as the irrelevant feature. Irrelevant information was the same in all experiments and consisted of digits. Digits are processed semantically in the parietal cortex [7,33]. When processing of the relevant feature depended on parietal cortex, as is the case for orientation processing (exp. 1 and 4), there was an effect of the digit’s magnitude on response times. Conversely, there was no effect of the irrelevant digit on the processing of color (exp. 2 and 3) or shape (exp. 5), which relies only minimally on parietal resources.

Importantly, alternative accounts can be ruled out. Firstly, there was no dependency of the effect on elapsed processing times. In exps. 3 and 5 conditions were created such that no SNARC effect was observed with similar or even longer response times than those observed in conditions which elicited a reliable SNARC effect (exp. 1). Secondly, in contrast with Ref. [22], mechanisms involved in object-based attention cannot account for the pattern of semantic influences in our experiments, with number as irrelevant information. Indeed, the SNARC effect did not depend on whether the relevant information consisted of a 2D object. With a 2D object as a target against the numerical background a SNARC effect was observed in an orientation identification task, but not in a shape discrimination task. Importantly, the 2D objects were of equal complexity in both tasks. Thirdly, there was no difference in dimensional overlap between the experiments [24,48]:

where a figure (triangle or line) had to be separated from the background. No figure–ground segregation was required in the color experiments. To judge the possibility that the SNARC effect results from this figure–ground segregation process rather than from the overlapping parietal neural structures between orientation and digit processing, the following experiment was set up. A figure was superimposed on the digit background, but in a situation where the task does not use parietal processing resources. Participants had to discriminate between a circle and a square. Shape discrimination has repeatedly been shown to rely on IT in the ventral stream [13,21,39].

Subjects made an average of 3.9% errors, with a maximum of 15.3% errors made by one subject. No speed–accuracy trade-off was present, as indicated by the absence of a negative correlation between RT and number of errors, computed over 18 data couples (nine numbers, separated for left and right responses), \( r = -0.06; n = 18; P < 0.40 \). Mean RTs of correct responses with the digits 1 to 9 were, respectively, 447, 458, 461, 462, 464, 466, 449, 459 and 495 ms. The regression analysis of repeated measures data resulted in the following equation (shown in Fig. 5):

\[
dRT = -18 - 0.36 \text{ magnitude.}
\]

No SNARC effect was found as there was no significant contribution of number magnitude to the pattern of left hand–right hand differences (\( t(19) = -0.35, \text{ S.D.} = 4.5, P < 0.3; \) six participants with a negative slope). This shows that the unattended digits were not processed up to the level of semantic information.
neither the processing of color, shape or orientation involves stimulus or response representations that are related to the numerical value represented by a digit.

Having excluded alternative explanations, we can conclude that the efficiency of feature-based attention is determined by the neural structures that are involved in the processing of both relevant and irrelevant information. If the processing of target and distracter make use of (partly) shared neural circuits then feature-based attention is less efficient compared to the situation where the processing of target and distracter is mediated by distinct circuits. These observations are in line with the view that feature-based attention modulates processing in feature-specific cortical areas [6,8,9,29,34,41]. Our results show that this relative enhancement is less efficient when there is neural overlap between target and distracter processing. Whether relative enhancement is accomplished by facilitation or by inhibition cannot be distinguished with the present paradigm.

Our current task, aimed at studying feature-based attention, naturally also implies a motor component: participants had to associate the visual information with either a left-hand or right-hand response. This type of task, then, involves learning an arbitrary rule to convert visual information into a motor command, as opposed to the more straightforward rules that underlie visually guided motor processing. Passingham et al. [40] have suggested that the former type of processing is regulated primarily by prefrontal cortex, whereas parietal cortex would be more involved in visually guided motor processing [36]. Thus, it may seem surprising at first that we find interference on parietal processing at all in our task with arbitrary visuo-motor associations. However, considering the fact that we kept the response dimension constant in all our experiments, it becomes clear that the SNARC effects must have emerged at a stage of information processing before motor control, that is, while encoding perceptual/cognitive representations. Representations of line orientation would compete with representations of number magnitude in parietal cortex. Consequently, the SNARC effect would already be implied in the neural code that prefrontal cortex receives from parietal cortex to compute the appropriate response. This leads us to speculate that stronger SNARC effects might be obtained if the response programming itself also takes place in parietal cortex, in a visually guided motor task. Before future research tests this hypothesis, however, we can already conclude from the present data that neural overlap between target and distracter processing in parietal cortex contaminates response times even in tasks with arbitrary stimulus–response association rules.

With ‘neural overlap’ we imply that the signal-to-noise ratio of the information coded by a neural unit, be it a single neuron or a cell assembly, can be directly affected by irrelevant afferents. For instance, the tuning curve of a neuron to a relevant feature (e.g. upward orientation) may be affected — flattened or even sharpened — depending on whether task-irrelevant input to the neuron coincides with the relevant input. Such influences would not occur if the irrelevant information uses a different neural pathway. This hypothesis borrows the concept of ‘overlap’ from the dimensional-overlap theory [24,48], but suggests that similarity of neural circuits, rather than similarity of stimulus and/or response, is the basis of interference. In this sense, it is an extension of the dimensional-overlap theory: it predicts interference in all of the cases of
dimensional overlap, but also in cases where dissimilar stimuli and/or responses are processed (at least in part) by the same neural structures.

Obviously, the present evidence from behavioral experiments can only indirectly support a hypothesis of neural overlap. We depend on the existing literature to identify neural circuits involved in discriminating color, shape or orientation, and in autonomous number processing. Event-related functional imaging and/or single-unit study using the present or a similar paradigm is required to provide direct evidence for our neural-overlap hypothesis. Some preliminary evidence, however, does already exist with primate prefrontal neurons in visual discrimination tasks [3,27]. For instance, Bichot and Schall showed that neurons in the frontal eye field coding the saccade target based on one visual feature (e.g. a red color) responded more clearly if the irrelevant feature (e.g. a square shape) indicated the previous saccade target than if it did not. In other words, an irrelevant stimulus–response association directly affects the signal-to-noise ratio of neurons whose code pertains to the same response dimension. Analogous processes of neural overlap in parietal cortex may account for our present data, with semantic influences from the number on feature processing in the dorsal pathway, but not in the ventral pathway.

Acknowledgements

Thanks are due to Marc Brysbaert, Mauro Pesenti and two anonymous reviewers for thoughtful comments. This research is supported by grant D.0353.01 of the Flemish Fund for Scientific Research. Johan Lauwereyns is supported by grant RFTF96L00204 from the Japanese Society for the Promotion of Science.

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