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Distinct neural networks for target feature versus dimension changes in visual search, as revealed by EEG and fMRI

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ABSTRACT

In visual search, responses are slowed, from one trial to the next, both when the target dimension changes (e.g., from a color target to a size target) and when the target feature changes (e.g., from a red target to a green target) relative to being repeated across trials. The present study examined whether such feature and dimension switch costs can be attributed to the same underlying mechanism(s). Contrary to this contention, an EEG study showed that feature changes influenced visual selection of the target (i.e., delayed N2pc onset), whereas dimension changes influenced the later process of response selection (i.e., delayed s-LRP onset). An fMRI study provided convergent evidence for the two-system view: Compared with repetitions, feature changes led to increased activation in the occipital cortex, and superior and inferior parietal lobules, which have been implicated in spatial attention. By contrast, dimension changes led to activation of a fronto-posterior network that is primarily linked with response selection (i.e., pre-motor cortex, supplementary motor area and frontal areas). Taken together, the results suggest that feature and dimension switch costs are based on different processes. Specifically, whereas target feature changes delay attention shifts to the target, target dimension changes interfere with later response selection operations.

Introduction

In visual search, changing the target *feature* across trials (e.g., from a red to a green target) or the target *dimension* (e.g., from a size target to a color target) typically leads to performance impairments (e.g., increased reaction time) relative to pairs of trials where target defining properties are repeated. For instance, in search for an "odd-one-out", changing the target feature from a smaller item to a larger item or from a red item to a green item slows responses to the target (e.g., Maljkovic and Nakayama, 1994; Becker, 2008a,b,c, 2010a,b). Similar switch costs occur when the stimulus dimension of the target is changed, for example, from a target differing in size to a target differing in color (e.g., a large to a red target; Müller et al., 1995). Originally, both types of intertrial effects were attributed to an attentional weighting mechanism. According to this *attentional biasing* account, selection of the target feature or the target dimension *primes* or *biases* attention to select the same feature or dimension on the next trial, by increasing the weights (or gains) of corresponding feature-specific and dimension-specific maps, respectively (e.g., Maljkovic and Nakayama, 1994; Müller et al., 1995).

In contrast to this early attention view of target switch costs, it has been proposed that they may reflect later processes involved in response selection (e.g., Cohen and Magen, 1999). According to a *response biasing account*, repeating the target could bias response selection mechanisms to repeat the response from the last trial as well, even when repetitions of the target feature and the response are statistically independent. For example, in a target present/absent search task, changing the target dimension (e.g., from a color to a size target) would automatically create a bias to change the response as well, which would lead to switch costs when the target changes but the instructed response is the same as in the previous trial (e.g., a target present response; Becker, 2008a, 2010a; Cohen and Magen, 1999; Mortier et al., 2005; Pollmann et al., 2006; Yashar and Lamy, 2011).

In line with the response biasing account, reaction times are often faster when both the target and response repeat than when only either the target or the response repeats (e.g., Hillstrom, 2000; Huang and Pashler, 2005; Meeter and Olivers, 2006; Müller and Krummancher, 2006; Töllner et al., 2008; Yashar and Lamy, 2011). Yet, at least with respect to feature changes, changing the response requirements does not completely eliminate target switch costs, indicating that they cannot be fully accounted for by response biasing (e.g., Hillstrom, 2000; Yashar and Lamy, 2011). As a consequence, most researchers to date advocate a *dual stage* account, which holds that target changes can incur costs both at an early attentional level and at a later, response-selection level (e.g., Meeter and Olivers, 2006; Mortier et al., 2005; Rangelov, Müller and Zehetleitner, 2011; Yashar and Lamy, 2011; Zeheitleitner et al., 2012).

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According to the dual stage account, feature and dimension changes will usually have the same impact on attention and response selection, and there is no reason to distinguish between them. In contrast to this prevalent view, recent findings suggest that feature and dimension changes may be categorically different and produce costs at different levels of information processing. Specifically, it appears that target feature changes mainly interfere with early attentional processes, whereas target dimension changes mainly influence later response selection processes (e.g., Becker, 2008a, 2010a). This *two-system hypothesis* is currently supported by three major findings. First, altering the target feature usually delays eye movements to the target (e.g., Becker, 2008a,b,c, 2013; McPeek et al., 1999), whereas changing the target dimension does not interfere with selection of the target but rather prolongs target dwell times (e.g., Becker, 2010a). Second, electroencephalography (EEG) studies have found that swapping the target and non-target features leads to large delays in the onset of the N2pc (~50 ms; Eimer et al., 2010), an electrophysiological marker for spatial attentional selection (e.g., Eimer, 1996; Luck and Hillyard, 1994), whereas dimension changes have only small effects on N2pc latencies (~8 ms; e.g., Töllner et al., 2008; 6 ms, Töllner et al., 2010, Rangelov et al., 2011) that cannot account for the substantial RT delay of 30–50 ms. Third, functional imaging data show that feature changes lead to an increased BOLD response in early visual areas (e.g., occipital cortex; Kristjansson et al., 2007), whereas dimension changes had no consistent effects on early visual areas, but instead led to increased activation of a dorsolateral pre-frontal network (DLPFC; Gramann et al., 2007, 2010; Pollmann et al., 2000, 2006; Weidner et al., 2002).

Although the above results are consistent with the view that feature switch costs are mainly due to an early attentional biasing mechanism whereas dimension switch costs are mainly due to a late response mechanism, the nature of the tasks used in these previous studies limits the extent to which a definitive conclusion can be made. Specifically, the results to date are based on a collection of studies that used different methods and stimuli to examine feature- versus dimension-based switch costs (e.g., Gramann et al., 2007, 2010; Kristjansson et al., 2007; Töllner et al., 2008, 2010; Pollmann et al., 2000, 2006; Weidner et al., 2002). Hence, it is unclear whether the observed differences between feature- and dimension-based switch costs were due to differences in the mechanisms tapped or the methods employed for each switch condition.

Here, we aim to directly compare feature- and dimension-based switch costs, using the same task, stimuli and methods in a within-subjects design. Specifically, changes of the target feature and the target dimension will be randomly generated within a continuous block, and the search displays will be identical across the different trial types (repeat, feature change, dimension change), ensuring that feature and dimension changes are not confounded with differences in search strategies or the stimuli. In the first experiment, we used EEG and in a second experiment, functional magnetic resonance imaging (fMRI) to assess whether feature and dimension switch costs in visual search arise at early or late levels of information processing. In both experiments, the participants' task was to indicate whether the target was present (66%) or absent (33%) from the display, and the experiments used the same stimuli and design. The target was defined as an odd-one-out that differed from the nontargets either in size or color: The nontargets were consistently orange, medium-sized disks, and the target could be either small or large, or red or yellow. Intertrial transitions from a color target to a size target or vice versa (e.g., small to red, yellow to large) were classified as *(across-)dimension changes*, and intertrial changes of the target size (e.g., small to large) or its color (e.g., red to yellow) were classified as *feature changes/within-dimension changes*. Trials in which the target from the previous trial was directly repeated were classified as *repeat trials* and served as a baseline against which the two types of switch costs were compared.

In Experiment 1, we recorded the EEG from participants and, following Töllner et al. (2008), assessed three ERP components: The *N2pc*, as a marker for attentional selection, the stimulus-locked LRP (lateralized readiness potential; *s-LRP*), as a marker for response selection/decision-making (e.g., Hackley and Valle-Inclán, 2003), and the response-locked LRP (*r-LRP*), as a marker for response execution (e.g., Eimer, 1998). The theoretically important question was whether target feature changes and target dimension changes would modulate the N2pc and LRPs in the same way or whether they would show evidence for dissociation. For the second experiment we employed an event-related fMRI design to identify the hemodynamic ('neural') correlates of target and dimension changes using the same stimuli and task as those used in the EEG experiment. Of primary interest was whether feature and dimension changes would affect entirely different brain regions, or a network of overlapping areas. Secondly, we sought to identify whether networks previously found to be involved in attention and response biasing would be tapped differently under feature versus dimension changes.

Materials and methods

Participants

Twenty participants with no history of psychiatric illness or neurological injury or illness participated in the study for monetary compensation ($10/h). Twelve participated in the EEG experiment, and eight in the fMRI experiment. All participants were naïve with regard to the purpose of the experiments and reported normal color vision and normal or corrected-to-normal visual acuity. All procedures were approved by the human ethics review committee at The University of Queensland.

Stimuli, design and procedure

In both experiments, the participants' task was to respond to the presence or absence of a target stimulus that differed in size or color from the nontargets. Target absent displays consisted of a central black fixation cross (size: 0.18° × 0.18°) and 6 medium-sized orange disks (diameter: 2.7°; RGB: 255, 94, 0; Lu'v': 43.8, 0.286, 0.538) presented against a white background at a distance of 9.2° from the central fixation cross. On target present trials, one of the nontargets was replaced with one of the possible targets. The color targets were either a yellow (RGB: 255, 155, 0; Lu'v': 59.8, 0.229, 0.546) or red (RGB: 255, 45, 0; Lu'v': 34.5, 0.342, 0.53) disk of the same size as the nontargets, and the size targets were either smaller (diameter: 1.9°) or larger (diameter: 3.9°) orange disks (the same color as the nontargets; see Fig. 1).

Targets were present on 66% of the trials, and the target type varied pseudo-randomly across trials (see below). When the target changed from a color target to a size target across trials, attention had to be shifted to a different stimulus dimension because the color target differed only in color, and the size targets differed only in size from the nontargets. Hence, trials in which a color target was preceded by a size target or vice versa were classified as *dimension change trials*. Trials in which the target color changed (e.g., from red to yellow) or in which the target size changed (e.g., from small to large) required shifting attention to a different feature within a stimulus dimension and were therefore classified as *feature (within-dimension) change trials*. Trials in which the target feature from the previous trial was directly repeated were classified as *repeat trials* and served as a baseline. Note that the search displays were identical across the different conditions (repeat, feature change, dimension change), so that differences between conditions cannot be attributed to physical differences between the targets (e.g., Kiss and Eimer, 2011).

The transition probabilities for target dimension and target feature (within-dimension) changes were 33.3%, respectively, to obtain equal numbers of trials in each of the conditions (repeat, feature change, dimension change). The target type (red/yellow/small/large) and location were chosen pseudo-randomly on each trial, with the restrictions that the target was presented equally often at the four lateral positions

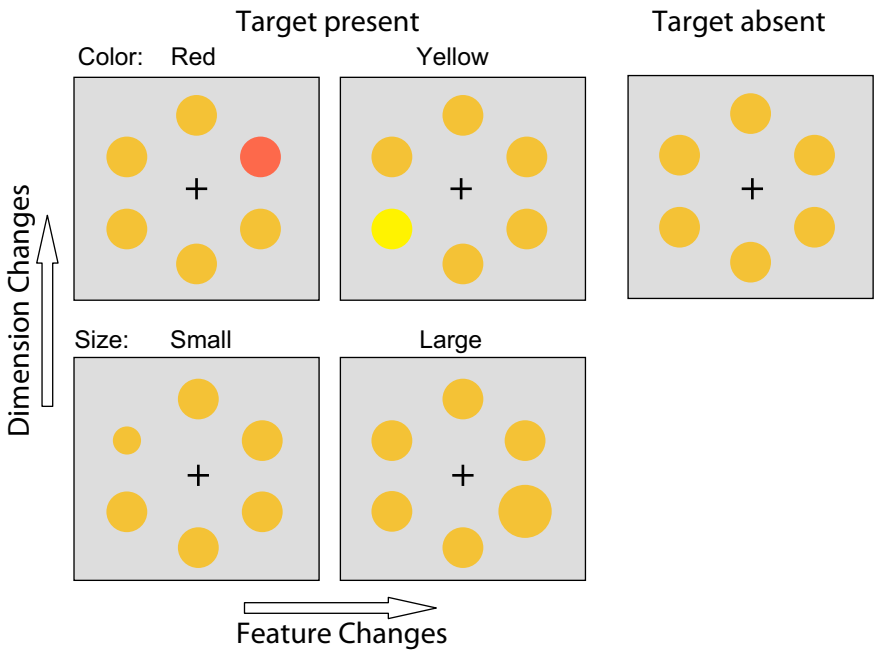

Fig. 1. Stimuli and design. Participants had to detect a target that differed either in color or size from the nontargets, and to indicate whether the target was present or absent. Trials in which the target changed from red to yellow or vice versa or from large to small or vice versa were classified as feature change trials, and trials in which the target changed from a larger or smaller target to a red or yellow target or vice versa as target dimension trials.

(never at the top or bottom position), and that the target location was never repeated on successive trials. Only target present trials that were preceded by target present trials were included in the analysis (e.g., Müller et al., 1995).

The search display was presented for 200 ms, followed by a fixation display that contained a small central fixation cross. After a fixed interval of 1000 ms (from the onset of the search display), a feedback tone (duration: 100 ms) indicated whether the response had been correct (1300 Hz tone) or wrong (500 Hz tone). In the EEG experiment, the intertrial interval was 500 ms, plus a random interval that varied between 0 and 350 ms. Participants responded with the index fingers of their right and left hand placed on two vertically aligned keys to target absent and target present trials, respectively, and the response mapping was reversed halfway through the experiment (for the purpose of assessing LRPs; see Eimer, 1998; Eimer et al., 2010). Participants completed at least 40 practice trials prior to the experiment (not recorded), and 840 experimental trials in each response mapping condition, yielding a total of 1680 trials.

In the fMRI experiment, the duration of the intertrial interval was randomly chosen from an exponential distribution ranging from 1500 ms to 7500 ms in steps of 1500 ms. Participants responded via a button box with the index and middle finger of their dominant hand. All participants completed at least 40 practice trials at a workstation outside the scanner prior to the experiment. In the scanner, participants completed 576 experimental trials, split into 8 sessions of 5.1 min each (72 trials, 204 scans per run). In both the EEG and fMRI experiments, participants were asked to maintain fixation on the central fixation cross during the entire trial, to avoid all body movements, and to respond as quickly as possible without committing any errors.

EEG recording and data analysis

The continuous EEG was recorded using a 64-channel ActiveTwo Biosemi EEG system (Biosemi Instrumentations, Amsterdam, Netherlands), digitized at 1024 Hz and re-sampled off-line to 250 Hz (using spline interpolation). All electrodes were mounted in an elastic cap corresponding to the 10–10 system Anon, 1994), and data were referenced off-line to the common average (Kayser and Tenke, 2010). Impedances were kept below 5 kΩ, and the raw EEG data was filtered off-line by means of a 40 Hz low-pass filter.

For the analysis of the N2pc and the s-LRP, the EEG was segmented from 200 ms before to 600 ms after target onset, and was averaged separately for all combinations of trial type (repeat, feature change, dimension change) and target hemi-field (left, right), or response hand (left, right), respectively. The epoched EEG was baseline corrected to the 200 ms pre-stimulus interval. Mean amplitudes were obtained in the 190–290 ms time window after target onset at lateral posterior electrode sites PO7 and PO8 for the N2pc and in the 300–500 ms post-stimulus time window at central C3 and C4 sites for the s-LRP.

For the analysis of the r-LRP, the EEG was initially segmented into 2000 ms epochs ranging from 1000 ms prior to 1000 ms post stimulus onset, so that the data could be baseline-corrected using the same 200 ms pre-stimulus baseline as that employed for the N2pc and the s-LRP. After the baseline-correction the EEG was re-segmented into epochs ranging from 600 ms before to 200 ms after response, and was averaged separately for each trial type (repeat, feature change, dimension change) and response hand (left, right). Mean amplitudes for the r-LRPs were acquired in the 150 to 50 ms time window prior to response at central electrode sites C3 and C4.

N2pc, s-LRP, and r-LRP onset latencies were determined separately for repeat, feature change, and dimension change trials using the jackknife procedure in which averaged ERP difference waves (ipsilateral ERPs subtracted from contralateral ERPs) are computed over subsamples of participants, systematically excluding one participant from the original sample (Miller et al., 1998; Ulrich and Miller, 2001). Onset latencies were defined as the point in time where the negative going deflection in the difference waveform of each subsample exceeded 40% of the N2pc peak amplitude (N2pc onset latencies; see Eimer et al., 2010 and Eimer et al., 2009, for an identical procedure), 50% of the s-LRP peak amplitude (s-LRP onset latencies; Miller et al., 1998), and 90% of the r-LRP peak amplitude (r-LRP onset latencies; Miller et al., 1998). Mean amplitudes and onset latencies were subjected to separate repeated-measures ANOVAs and two-tailed *t*-tests using the statistical software package SPSS. Statistical *t* and *F* values comparing jackknifed onset latencies were corrected according to the formulas

described by Miller et al. (1998) and Ulrich and Miller (2001), respectively, and were indicated with the labels 't_c' and 'F_c'.

fMRI

Images were acquired with a 3 T Siemens Trio scanner equipped with a 12-channel head coil. Anatomical scans were acquired using a rapid gradient-echo sequence with 1 mm isotropic voxels. Functional images were collected in 27 transverse slices of 3 mm (distance: 33%) with echo planar imaging [TR = 1500 ms, TE = 31 ms, FA = 90°, FOV = 192 mm, matrix: 64 × 64, voxel size: 3 × 3 × 3 mm]. In each session, participants completed 8 event-related runs.

Images were analyzed using FSL (FMRIB, Oxford, UK). Data were first motion-corrected and slice time-corrected, and then convolved with a 7 mm FWHM Gaussian Kernel. As in Pollmann et al. (2006), event-related BOLD signal changes were modeled with a set of 3 basis functions (FMRIB's linear optimal basis sets; e.g., Jenkinson et al., 2012; Woolrich et al., 2009; Smith et al., 2004). To assess differences between the trial types (repeat, feature change, dimension change), we first compared dimension change trials to repeat trials, and feature change trials to repeat trials. Then, to extract differences that are specific to the different kinds of intertrial changes, we contrasted dimension change trials with feature change trials. Both contrasts were computed by linearly combining the respective contrasts from lower-level analyses across sessions and subjects (e.g., Pollmann et al., 2006), and by using permutation testing (FSL's randomize function; 5000 permutations; Hayasaka and Nichols, 2003). All voxel-wise statistical comparisons are reported at an FDR-corrected alpha level of .05, and only clusters with a minimum voxel cluster size of >27 voxels are reported.

Results

Data screening

Only target present trials that were preceded by target present trials were included in the analysis. Trials with delayed (>1000 ms) or anticipatory (<200 ms) responses were excluded from the data analyses, leading to a loss of 1.27% of the data in the EEG experiment, and 2.15% in the fMRI experiment. Moreover, in the EEG experiment, trials with artifacts (eye movements exceeding +/− 30 μV in the HEOG channels; blinks exceeding +/− 60 μV at Fp1/2; muscular movements exceeding +/− 80 μV in all other channels) were excluded (7.4%) from the analysis of event-related potentials (ERPs), leaving on average 219, 199 and 204 trials per participant for the ERP analysis of repeat, feature change and dimension change trials, respectively.

Mean response times and errors

Experiment 1 — EEG

Analysis of the mean response times (RTs) showed significant costs of changing the target feature and the target dimension between trials: A repeated-measures ANOVA with the factor of trial type (repeat, feature change, dimension change) showed that mean RT significantly differed between the three conditions, $F(2,22) = 35.4$, $p < .001$, $\eta^2 = .76$. Compared with repeat trials (M = 513 ms), both changes of the target feature and the target dimension significantly delayed RT, by 24 ms and 37 ms, respectively, both $ts(11) = 7.0$, $p < .001$. Dimension switch costs were also significantly larger than feature change costs, $t(11) = 2.8$, $p = .017$.

The same results were obtained for the arcsine-transformed error scores: There were significant differences between the trial types, $F(2,22) = 20.7$, $p < .001$, $\eta^2 = .65$. Compared with repeat trials (M = 5.6%), more errors were committed when the target feature changed (M = 7.4%), $t(11) = 2.5$, $p = .031$, and when the target dimension changed (M = 11.1%), $t(11) = 5.2$, $p < .001$. In addition, error scores were higher on dimension change trials than on feature change trials, $t(11) = 5.7$, $p < .001$ (Fig. 2).

Experiment 2 — fMRI

The results of the fMRI experiment displayed a similar pattern: The ANOVA showed significant RT differences between the trial types (repeat, feature change, dimension change), $F(1,7) = 27.9$, $p < .001$, $\eta^2 = .80$. Compared with repeat trials (M = 479 ms), changing the target feature led to switch costs of 26 ms, $t(7) = 5.7$, $p = .001$, and changing the target dimension led to switch costs of 34 ms, $t(7) = 7.1$, $p < .001$. The respective switch costs did not differ significantly from one another, $t(7) = 1.5$, $p = .17$. The same analyses computed over the arcsine-transformed error scores showed significant differences between the conditions, $F(1,7) = 8.3$, $p = .004$, $\eta^2 = .54$. Compared with repeat trials (M = 3.3%), more errors were committed on feature change trials (M = 6.7%), $t(7) = 3.8$, $p = .007$, and on dimension change trials (M = 6.4%), $t(7) = 4.2$, $p = .004$, with no differences between feature and dimension change trials, $t < 1$ (see Fig. 2).

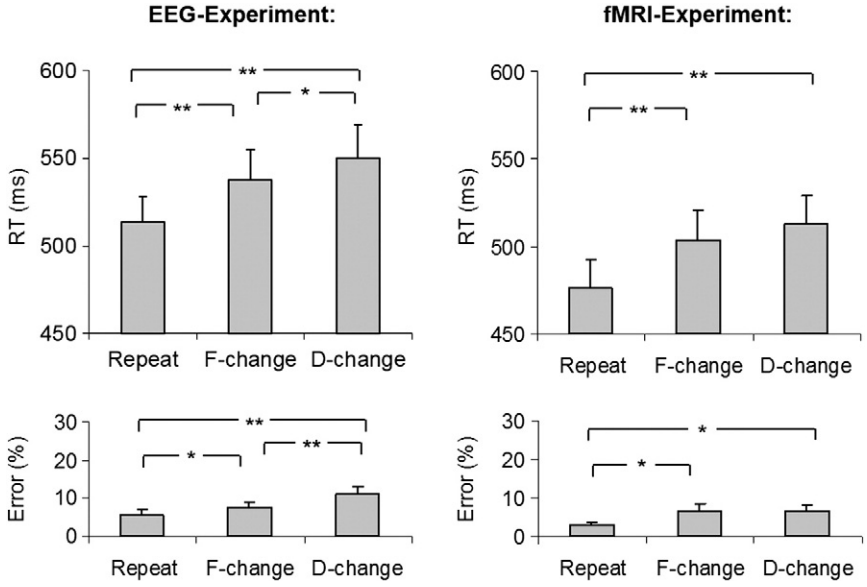

Fig. 2. Mean RT and errors for feature and dimension changes. Mean RT and error scores on repeat trials, feature change trials and dimension change trials, depicted separately for the EEG experiment (left panels) and the fMRI experiment (right panels). F-change = Feature Change Trials; D-change = Dimension Change Trials. *$p \leq .05$; **$p \leq .001$.

In sum, both experiments showed significant switch costs for changes of the target dimension and the target feature. In the EEG experiment we additionally found higher costs for changes of the target dimension than the target feature. This is a common result (e.g., Kumada, 2001; Mortier et al., 2005), which was however not observed in the fMRI experiment — possibly because the longer ITIs selectively reduced across-dimension switch costs. In line with this possibility, Maljkovic and Nakayama (1994) reported that feature priming effects survive long ITIs of ~12 s, whereas no such long-lasting effects have been reported for across-dimension switch costs.

On the other hand, the pattern of switch costs did not differ significantly between experiments. Comparing the mean RT with a 2 (experiment: 1, 2) × 3 (trial type: repeat, feature change, dimension change) mixed-model ANOVA yielded only a significant main effect of the trial type, $F(2,36) = 58.9$, $p < .001$, but no interaction with experiment, $F < 1$. Independent t-tests computed over the data of each trial type (repeat, feature change, dimension change) similarly revealed no differences between the experiments, all $ts < 1.6$, $ps > .23$, indicating that switch costs of the target feature and dimension did not differ across experiments.

Stimulus-specific switch costs: experiments 1 (EEG) and 2 (fMRI)

To examine whether feature and dimension switch costs reliably occurred for all inter-trial transitions, data were pooled across experiments and RT switch costs were examined separately for each target stimulus (red, yellow, small, large) and the previous target type ($n - 1$ red, $n - 1$ yellow, $n - 1$ small, $n - 1$ large). As shown in Table 1, significant switch costs (computed as RT on a switch trial − RT on a repeat trial) were obtained for all target types and inter-trial transitions, all $ts > 3.4$, $ps < .003$.

EEG results & discussion: N2pc, s-LRP and r-LRP

N2pc

The top panel of Fig. 3 shows grand-average ERPs elicited at electrode sites PO7/8 contra- and ipsilateral to the hemi-field of the target, separately for repeat, feature change and dimension change trials. The graphs suggest that all three experimental conditions yielded N2pc components of similar size. This observation was statistically confirmed when ERP mean amplitudes, measured in the 190–290 ms post-stimulus time window, were subjected to a repeated-measures ANOVA with the factors trial type (repeat, feature change, dimension change) and laterality (ipsilateral, contralateral). The ANOVA revealed a significant main effect of laterality, $F(1,11) = 14.1$, $p = .003$, but no effect of trial type, $F(2,22) = 2.4$, $p = .115$, nor a reliable interaction, $F < 1$. The finding of similar N2pc amplitudes on repeat (M = −0.6 μV), feature change (M = −0.6 μV) and dimension change trials (M = −0.6 μV) shows that attention was shifted to the target in all three conditions.

Table 1
Mean RT separately for each inter-trial transition.

Target color	$n - 1$ target color			
	$n - 1$ red	$n - 1$ yellow	$n - 1$ small	$n - 1$ large
Red	498 [12.1]	523 [11.8]	530 [12.6]	519 [12.5]
Switch cost	–	*25 ms***	*32 ms***	*21 ms**
Yellow	488 [12.8]	463 [11.9]	499 [15.2]	495 [14.8]
Switch cost	*23 ms***	–	*34 ms***	*30 ms***
Small	573 [15.7]	565 [15.5]	527 [11.7]	554 [14.3]
Switch cost	*47 ms***	*38 ms***	–	*27 ms***
Large	555 [12.4]	553 [14.7]	541 [13.7]	513 [11.8]
Switch cost	*42 ms***	*40 ms***	*29 ms***	–

Note. Numbers in brackets denote the standard error of the mean. Switch costs are computed as the difference between RT on trials with different target attributes and direct repeat trials. *$p = .0025$, **$p < .001$, as per two-tailed t-test.

To examine whether changes of the target feature or dimension delayed attention shifts to the target, N2pc onset latencies were determined on the basis of difference waves (obtained by subtracting ipsilateral from contralateral ERPs). Fig. 3 (left middle panel) shows these difference waveforms, separately for the three trial types (repeat, feature change, dimension change). Comparing onset latencies (determined at 40% of the N2pc peak amplitude) across conditions with a one-way ANOVA showed that the N2pc onsets differed significantly between repeat, feature change, and dimension change trials, $F_c(2,22) = 5.0$, $p = .016$. Paired t-tests showed that onset latencies on feature change trials (236 ms) were significantly delayed compared to repeat trials (211 ms), $t_c(11) = 3.4$, $p = .006$, and dimension change trials (214 ms), $t_c(11) = 3.3$, $p = .007$. Onset latencies for repeat and dimension change trials did not significantly differ, $t_c < 1$.[1] Thus, attention shifts to the target were delayed by changes of the target defining feature only, whereas changes of the target defining dimension did not affect the speed of target selection. It is also worth noting that, the feature switch costs on N2pc latencies (25 ms) almost perfectly matched the size of behavioral feature switch costs (26 ms).

s-LRP

The bottom panel of Fig. 3 displays s-LRP difference waveforms at electrode sites C3/4 separately for repeat, feature change, and dimension change trials. All s-LRPs were of similar size, as was demonstrated by a one-way ANOVA on mean amplitudes measured in the 300–500 ms post-stimulus time window, $F < 1$.

To examine whether feature and dimension changes produce delays in response selection processes, we compared s-LRP onset latencies (defined as 50% of the s-LRP peak amplitude) between repeat, feature change and dimension change trials using a one-way ANOVA. The results showed a main effect of trial type, $F_c(2,22) = 5.8$, $p = .010$, reflecting that s-LRP onset latencies were significantly delayed on dimension change trials (310 ms) compared to repeat trials (282 ms), $t_c(11) = 3.0$, $p = .012$, whereas feature change trials (298 ms) differed neither from repeat trials, $t_c(11) = 2.1$, $p = .061$, nor from dimension change trials, $t_c(11) = 1.6$, $p = .145$. Numerically, the dimension change costs on the s-LRP onset latencies (28 ms) can account for a large portion of the RT costs (41 ms). By contrast, the non-significant s-LRP onset delay for feature changes relative to repeat trials cannot be interpreted as arising from response selection processes. Within the limits imposed by criterion-based latency estimates, this delay reflects the propagation of the initial delay in shifting attention to the target (N2pc onset delay; see e.g., Eimer, 1996; Töllner et al., 2008; Wiegand et al., 2013). Taken together, the pattern of ERPs supports the two-system view (e.g., Becker, 2010a,b) — changing the target feature leads to costs on the level of target selection (N2pc), whereas target dimension changes produce costs on the level of response selection (s-LRPs).

r-LRP

Fig. 3 (right central panel) shows difference waveforms at electrode sites C3/4 locked to the time of the response. A repeated-measures ANOVA computed over the mean amplitudes in the 150–50 ms time window prior to response showed no significant differences between

[1] Additional analyses using an N2pc onset criterion of 0% (reflecting the point in time when each N2pc difference wave diverged from 0) and of 50% computed over the jackknifed data revealed exactly the same results. The ANOVA on N2pc onset latencies calculated by means of a 0% criterion revealed a significant main effect of trial type, $F_c(2,22) = 6.6$, $p = .004$. The N2pc on feature change trials (207 ms) was delayed relative to the N2pc on repeat (174 ms), $t_c(11) = 3.0$, $p = .001$, and dimension change trials (182 ms), $t_c(11) = 3.2$, $p = .009$. N2pc onset latencies were statistically the same on repeat and dimension change trials, $t < 1$. The same pattern was found on N2pc onset latencies measured with a 50% onset criterion. The ANOVA revealed a main effect of trial type, $F_c(2,22) = 5.6$, $p = .007$, with delayed N2pc latencies on feature change (240 ms) relative to repeat (215 ms), $t_c(11) = 3.7$, $p < .001$, and dimension change trials (218 ms), $t_c(11) = 3.3$, $p = .007$, and no differences between repeat and dimension change trials, $t_c < 1$.

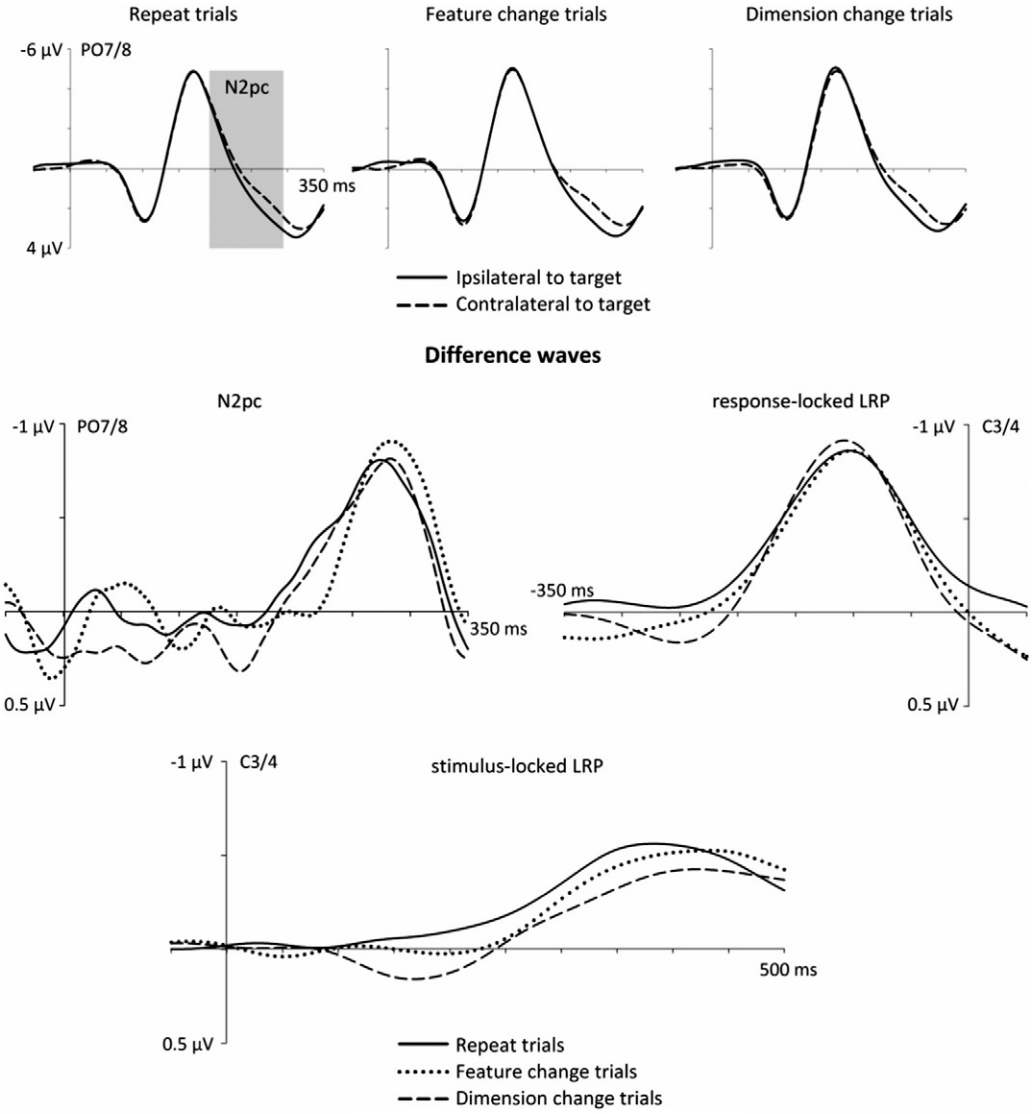

Fig. 3. Results of EEG experiment: N2pc, s-LRP and r-LRP. Grand-average event-related potentials (ERPs, in microvolt) measured in the EEG experiment, elicited at electrode sites PO7/8 contra- and ipsilateral to the location of a target (top panel). The middle and bottom panels show difference waveforms obtained by subtracting ipsilateral from contralateral ERPs at sites PO7/8 (N2pc) and C3/4 locked to the onset of the stimulus (s-LRP) and the response (r-LRP), separately for repeat, feature change, and dimension change trials.

the different trial types, indicating that the r-LRPs were of equal magnitude on repeat, feature change and dimension change trials, $F < 1$.

To examine whether changing the target feature or dimension would delay response execution processes, we compared r-LRP onset latencies (determined at 90% of the r-LRP amplitude) on repeat, feature change and dimension change trials with a one-way repeated-measures ANOVA. The analysis showed that r-LRP onset latencies did not differ significantly from each other, $F_c < 1$ (repeat: −78 ms; feature change: −79 ms; dimension change: −85 ms). Hence, the r-LRPs were not affected by changes of either the target feature or the response. An effect of target changes on the r-LRP was not predicted, because the r-LRP onsets typically reflect the time-course of executing a response (e.g., Töllner et al., 2008), and we varied only the sensory characteristics of the target, not the difficulty of response execution (i.e., all conditions required a simple key-press response).

Collectively, the results of the EEG experiment suggest that switch costs occurring as a result of changes of the target feature (e.g., red/yellow) and the target dimension (e.g., red/large) may not reflect the same underlying mechanism (e.g., Becker, 2008a, 2010a). Whereas feature changes predominantly delay attention shifts to the target, changes of the target dimension mainly interfere with later, response selection processes. This dissociation is supported by two major findings: First, the onset of the N2pc, which reflects the time required to shift attention to the target, was selectively delayed for feature change trials, not dimension change trials. Second, the onset of the s-LRP, which reflects the time-course of response selection, was delayed for target dimension changes, whereas the s-LRP on feature change trials was not delayed beyond expectations (i.e., more than the initial N2pc delay). These results support the two-system view (e.g., Becker, 2008a, 2010a), that changing the target feature leads to costs on the level of target selection (N2pc), whereas target dimension changes produce costs on the level of response selection (s-LRPs).

The present findings, however, should not be taken to mean that the respective other processes didn't contribute to RT switch costs observed in either condition. For instance, on dimension change trials, the s-LRP onset delay was numerically smaller than the RT switch cost (by 13 ms), and there was a small and non-significant delay in the N2pc onset, allowing for the possibility that early perceptual processes may have contributed to dimension change costs. Similarly, it remains possible that response selection costs contribute to feature change costs (although this assumption seems unnecessary, as the delay in attention shifts (N2pc onset delay of 25 ms) can fully explain the RT switch cost

(of 26 ms)). What seems to be clear from the present data is that the bulk of feature and dimension change costs reside in early attentional processes versus response-selection processes, thereby supporting the two-system account (Becker, 2010a).

fMRI results & discussion

The results of the fMRI experiment are depicted in Figs. 4A–C and Table 2. We first contrasted feature change trials and dimension change trials separately with repeat trials (Dimension Change > Repeat and Feature Change > Repeat). Differences between the two types of switch costs were further analyzed by directly comparing target dimension changes and feature changes (Dimension Change > Feature Change and Feature Change > Dimension Change). The results of the non-parametric permutation tests are reported at an FDR-corrected alpha level of .05 (see Table 2; all uncorrected *p*s < .001).

Dimension changes

Comparing dimension change trials to repeat trials (Dimension Change > Repeat; Fig. 4A, blue clusters) showed increased activation of parietal areas surrounding the superior parietal lobule (SPL), and the left premotor cortex (BA 6). Replicating the findings of Pollmann et al. (2000, 2006), we also found activation in the right frontal pole and the right orbito-frontal cortex as well as bilaterally in middle frontal areas.

Comparing dimension change trials with feature change trials (Dimension Change > Feature Change) revealed no significant differences in the SPL, but significant differences in two locations of the right frontal pole, bilateral premotor areas, as well as in the right supplementary motor area (SMA). In addition, this contrast revealed higher activation in the right insula, the right fusiform gyrus, and the left middle frontal gyrus (see Fig. 4A, red clusters).

Feature changes

Comparing feature change to repeat trials (Feature Change > Repeat; Fig. 4B, green clusters) also led to significant activation of the left precuneus, but otherwise showed a markedly different results pattern. Consistent with the results of Kristjansson et al. (2007), feature changes led to significant activation of occipital areas, compared to repeat trials. In addition, significant activation of the right intraparietal lobule (IPL) was observed.

Compared with dimension change trials, feature changes (Feature Change > Dimension Change) led to more activation in right and left occipital areas. Moreover, feature change trials led to significantly more activation in the dorsal part of the IPL (see Fig. 4B, red clusters).

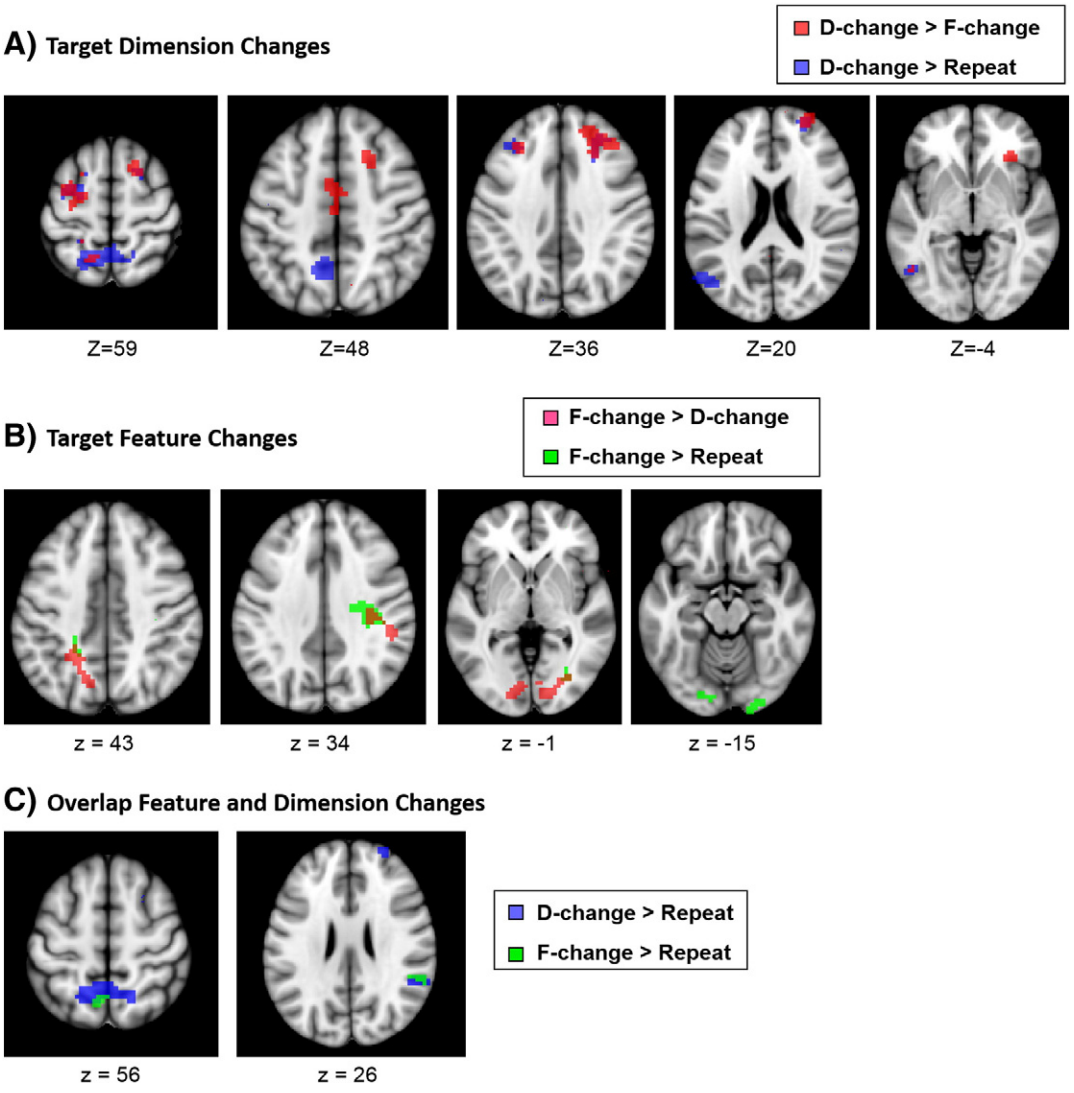

Fig. 4. Results of the fMRI experiment. Changing the target dimension led to an increased BOLD response in SPL, frontal areas, and lateral occipital cortex (A). Changing the target feature led to higher activation of occipital areas and posterior parietal areas including SPL and IPL (B). Two regions showed significant activation for both target feature and target dimension changes, the left SPL (left image) and the right TPJ/IPL (right image) (C). All images are in neurological convention (left side = left hemisphere; right side = right hemisphere).

Table 2
Size and MNI coordinates for significant clusters, Experiment 2.

Extent (voxels)	MNI Coordinates (mm)			Structure
	x	y	z	
Dimension change > repeat				
279	−12	−54	54	L precuneus cortex/SPL
84	−30	−3	63	L superior/precentral frontal gyrus
53	−54	−66	18	L lateral occipital cortex
48	60	−45	30	R angular/supramarginal gyrus/IPL
39	24	27	33	R middle frontal gyrus
39	27	57	24	R frontal pole
34	−30	30	36	L middle frontal gyrus
29	−6	27	24	L cingulate cortex (anterior division)
28	−51	−66	−6	L insular cortex
Dimension change > feature change				
122	27	36	33	R frontal pole/middle frontal gyrus
110	−21	−9	66	L superior/precentral frontal gyrus
62	21	15	48	R superior frontal gyrus
59	30	57	18	R frontal pole
54	−6	0	48	L supplementary motor cortex
52	27	27	3	R insular cortex
37	24	−42	−18	R temporal occipital fusiform gyrus
28	−30	30	36	L middle frontal gyrus
Feature change > repeat				
102	−12	−66	45	L precuneus cortex/SPL
101	15	−87	−3	R occipital pole
78	51	−33	36	R parietal/supramarginal gyrus/IPL
70	−15	−87	3	L occipital pole
Feature change > dimension change				
119	36	−24	33	R IPL
30	21	−96	−12	R occipital pole
28	−12	−87	−15	L occipital pole

In sum, the results of the fMRI experiment showed that changes of the target dimension and the target feature led to activation of different and largely separable brain regions. In fact, the results reveal only two regions that were both more strongly activated by changes of the target feature and the target dimension (compared to repeat trials); the left SPL, and the right TPJ/IPL (see Fig. 4C). Apart from this, there was no overlap between regions that were active in feature change versus dimension change trials, indicating that feature changes and dimension changes have separable effects and may affect visual search at different levels of processing.

General discussion

In the present study we directly compared trial-to-trial target feature changes to dimension changes in a simple target detection task. The results were clear: Feature changes delayed attention shifts to the target, whereas target dimension changes mostly interfered with later, response selection processes. Thus, the results support an attentional account of feature change costs and a response biasing account for dimension switch costs, in line with the two-system hypothesis (Becker, 2010a).

Two findings from the EEG support this two-system account: First, target feature changes significantly delayed the onset of the N2pc (an electrophysiological marker for attention shifts; Eimer, 1996), whereas dimension changes did not interfere with target selection. Second, dimension changes led to a significant delay in the s-LRP (an electrophysiological marker for response-selection; Hackley and Valle-Inclán, 2003), indicating that dimension changes interfered with response selection.

The fMRI study similarly showed that feature and dimension changes have dissociable effects as feature and dimension change costs were largely associated with different brain areas. There were only two regions showing a moderate overlap for feature and dimension costs (left SPL and right IPL), indicating that the associated processes are largely driven by different underlying neural substrates. Specifically, target dimension changes led to higher activation in pre-motor and other frontal areas, regions that have previously associated with response-selection processes (Dux et al., 2006, 2009; Marois et al., 2006), and feature changes led to higher activation in occipital areas, previously implicated in featural attention processing (e.g., Serences et al., 2005).

Theoretical implications

The present study represents the first successful attempt to study the electrophysiological and systems-level hemodynamic (neural) correlates of feature and dimension changes within a single task with the same set of stimuli used for all the conditions. Specifically, within each experiment, feature and dimension changes of the target were varied randomly within a block, which allowed directly comparing switch costs arising from feature changes versus dimension changes in the absence of confounds arising from differences in the stimuli, task or participants. Moreover, although fMRI and ERP measurements were conducted in separate experiments and with different subjects, the EEG results can inform the interpretation of fMRI results and vice versa, which allows us to interpret the results regarding the neural correlates of feature and dimension switch costs with high temporal and spatial resolution.

Of note, the present findings closely match the results of previous studies investigating target dimension and target feature changes, despite the fact that these studies used different tasks (i.e., compound search task) and stimuli (e.g., Eimer et al., 2010; Kristjansson et al., 2007; Pollmann et al., 2006; Töllner et al., 2008). Yet, previous work often interpreted the findings very differently, with the greatest discrepancy being that switch costs due to target dimension changes were often attributed to early attentional processes (e.g., Pollmann et al., 2000, 2006; Töllner et al., 2008). The results of the present study are inconsistent with this hypothesis, since only feature changes but not dimension changes delayed early attentional processes (i.e., N2pc onset). The discrepancy is however not in the results: Interestingly, an examination of the literature reveals that previous studies had similarly failed to show sufficiently large N2pc onset or peak latency delays that could explain across-dimension switch costs (e.g., Töllner et al., 2008, 2010), whereas N2pc delays due to changes of the target feature matched the behavioral costs, reflecting delays in shifting attention to the target (e.g., Eimer et al., 2010). However, because previous studies lacked the means to directly compare effects of feature and dimension changes, small N2pc peak latency delays were still interpreted as evidence that dimension switch costs were due to delays in shifting attention to the target (e.g., Töllner et al., 2008). In the present study, we were able to directly compare the effects of dimension changes to feature changes, which revealed that only feature changes were associated with attentional switch costs.

Previous fMRI studies on dimension changes found significant activation of multiple posterior brain areas (e.g., Pollmann et al., 2000: fusiform gyrus, lateral occipital gyrus, superior/middle temporal gyrus, SPL and precuneus; Pollmann et al., 2006: IPS, fusiform gyrus, striate/peristriate cortex and posterior putamen/claustrum) that have been implicated in early attentional processes (Corbetta et al., 1993, 1995, 2000; Corbetta and Shulman, 1999; Kelley et al., 2008; Macaluso et al., 2000; Nobre et al., 1997; Vandenberghe et al., 2000; Yantis et al., 2002). Hence, it was concluded that dimension changes interfere with attention shifts to the target. Moreover, significant activation of frontal areas and especially the dorso-lateral pre-frontal cortex (DLPFC) was interpreted as evidence that DLPFC is involved in re-assigning attentional weights to different stimulus dimensions (e.g., Pollmann et al., 2000). In the present study, we similarly found activation in multiple frontal brain areas (i.e., right frontal pole, right middle frontal gyrus, left precentral gyrus), as well as posterior brain areas (i.e., left lateral occipital cortex and SPL). However, we cannot interpret the latter results as reflecting early attentional switch costs, because the results from the EEG study showed that dimension changes did not interfere with

attention shifts to the target. Instead, target dimension changes interfered with response selection (as reflected in the significant s-LRP onset delay). This indicates that the activation of frontal and parietal areas observed at target dimension changes has to be interpreted within the framework of a response selection account.

According to a response selection hypothesis, stimulus-to-response mappings (SR-mappings) that are automatically created in the course of the experiment create a bias to change the response when the target dimension changes, which leads to activation of an incorrect response on change trials (i.e., target absent response when target present response is required; e.g., Becker, 2010a; Cohen and Magen, 1999; Mortier et al., 2005). According to this account, the parietal and frontal areas as well as the ACC that were found to be active at dimension changes could be involved in resolving conflicts in response selection.

In line with this contention, previous studies have shown that posterior parietal areas are involved in governing SR-mappings (e.g., Rushworth et al., 1997, 2001; Wager et al., 2005). For instance, Rushworth et al. (2001) examined effects of changing visual selection rules (attend to shape/color) versus response rules. Visual changes were associated with activation in posterior lateral intraparietal sulcus and the parieto-occipital region, whereas changes of the response rules led to activation in the medial intraparietal sulcus, posterior SPL, dorsomedial parietal cortex, and the anterior lateral intraparietal sulcus. Rushworth et al. (2001) concluded that modulation of the SPL and the medial parietal cortex is related to changes of the response rules, whereas the core visual selection areas are located further in the intraparietal sulcus. The present findings dovetail with those of Rushworth et al. (1997, 2001), especially in that both studies showed minimal overlap between areas involved in visual selection versus response conflict, and support their conclusion that SPL has a role in maintaining and applying the correct SR mappings (or visuomotor rules, as they are called in Rushworth et al., 2001).

In addition, we found that dimension changes significantly increased activation in the pre-motor area/supplementary motor area (SMA) and other frontal areas (e.g., DLPFC). The activation in the pre-motor areas may be linked to the incorrect response being activated, whereas the other frontal activations most likely reflect the need to re-organize SR-mappings. In line with this interpretation, Wager et al. (2005) showed that a go/no-go task, which required withholding of incorrect responses, led to significant increases in the brain areas that closely matched those activated by target dimension changes; viz. the DLPFC, right anterior PFC, premotor cortex, SMA (as well as posterior and inferior parietal regions; compare Pollmann et al., 2000; see also Dux et al., 2006, 2009; Filmer et al., 2013a,b; Tombu et al., 2011).

In sum, the results of the target dimension changes can be interpreted in a similar manner to previous studies that investigated genuine response conflicts: Whereas frontal and parietal areas have a central role in governing SR mappings, pre-motor areas are involved in a more executive stage of applying SR mappings (e.g., Wise et al., 1997; Wise and Murray, 2000).

Proponents of the early attentional view of dimensional switch costs could argue that dimension changes also led to significant activation of the occipital cortex, close to the (functionally defined) lateral occipital cortex (LOC), which could be interpreted as a correlate for early attentional switch costs (see Pollmann et al.'s (2000) interpretation of activation in the lateral occipital sulcus). As noted above, however, this interpretation is at odds with the results from the EEG study (Experiment 1). Moreover, the feature change condition clearly showed evidence for attentional switch costs without significant activation of those occipital areas that were active during dimension changes. This indicates that activation of this lateral occipital area may not reflect attentional switch costs. Instead, target feature changes led to significant activation of early visual areas (viz., right and left occipital poles). These results mimic the findings of Kristjansson et al. (2007) and corroborate their conclusion that feature changes produce attentional switch costs that are reflected in early visual areas.

Previous studies can potentially shed light on how the significant activation of lateral occipital areas could be interpreted without assuming that dimension changes affect attentional processes. For instance, in an eye tracking study, Becker (2010a,b) found that target dimension changes delayed processes associated with object identification, since the target dwell times were selectively prolonged for target dimension changes, whereas eye movements to the target were not delayed (Becker, 2010a). Significant activation of the occipital cortex close to the LOC could thus be due to the fact that changing the target dimension prolongs target identification *after* the target has been visually selected, but possibly prior to selecting the response (e.g., Becker, 2008a, 2010a; Müller and Krummancher, 2006). This interpretation is also in line with the view that LOC is mostly involved in processes of object recognition and object identification (e.g., Grill-Spector et al., 2001).

Hence, a plausible account of feature and dimension changes would be that changing the target dimension across trials leads to (1) costs in visual identification of the target that commence after the attention has been shifted to the target, reflected in the significant activation of LOC, and (2) a response selection bias to change the response (compared to the last trial), reflected in the significant activation of frontal areas and especially the pre-motor area (see Table 2 and Fig. 4). By contrast, changing the target feature within a dimension across trials predominantly delays attention shifts to the target, as is probably reflected in the significant activation of the right and left occipital cortex (see also Kristjansson et al., 2007).

Explaining switch costs at feature and dimension changes

The present results provide the first neurophysiological evidence for the two-system hypothesis that target feature changes but not dimension changes interfere with attentional selection of the target. How can we explain that feature changes cause attentional switch costs only within a stimulus dimension but not across different dimensions?

We propose that this result can be explained by a *nontarget biasing* account, which assumes that an attentional bias to a given feature will delay target selection only when the bias favors selection of a nontarget. According to most theories of top-down control, attention is rather broadly biased to the target feature; for instance, redder or yellower rather than the exact color values (e.g., Becker, 2010b; Becker et al., 2013; Duncan and Humphreys, 1989; Wolfe, 1994). Such a broad selection criterion can lead to erroneous selection of the nontargets when the target feature changes, because the nontargets are now more similar to the previous target than the actual target. For instance, when a target on the previous trial had been red among orange nontargets, attention will be biased to select redder or red-similar items on the next trial(s). This leads to erroneous selection of the nontargets when the next target is yellow, because the orange nontargets are now more similar to the previous target (redder). Several studies have shown that target feature changes indeed bias attention and the gaze to the nontargets (e.g., Becker, 2008a,b,c, 2010a,b, 2013; McPeek et al., 1999).

Under this framework, changing the target dimension does not produce any attentional costs, because an attentional bias to select larger or smaller items does not favor selection of the nontargets over the target when these differ only in color (or vice versa). For example, when the previous target had been larger, the bias to select larger items does not translate into a preference for red, orange or yellow items. In the absence of an attentional bias to select the nontargets, the target can be quickly selected simply because it is the only salient item in the display — in short: because it has no competition.[2]

[2] According to the nontarget biasing account, changing the target dimension could still produce attentional switch costs — for instance, when the target has a very low feature contrast and target–nontarget discrimination is very difficult. However, changing the target feature should produce still larger attentional switch costs than dimension changes, if the feature change renders the nontargets similar to the previous target.

The nontarget biasing account can also explain some puzzling findings, viz. that mere changes in the target color or the non-target color alone have previously failed to show N2pc onset delays, whereas partially swapping the target and non-target features has shown N2pc onset delays that matched those observed in a full-swap condition (Eimer et al., 2010, Experiment 2). In studies that failed to show significant switch costs at mere target feature changes, colors from different categories were used (red, green, blue; e.g., Eimer et al., 2010). Presumably, a bias for a red target item from the previous trial does not translate into a bias to select (green or blue) nontargets when the color of the target changes (to blue or green). Partially swapping the target and nontarget colors (e.g., from red target among green nontargets to green target among blue nontargets; or blue target among red nontargets) will bias attention to the nontargets, either because these now have the color of the previous target, or because the target has inherited the color previously associated with the nontargets and is consequently inhibited (which in turn increases competition from the nontargets).

A second important question is why only changes of the target dimension and not the target feature would create response conflicts and delay response selection. Cohen and Magen (1999) proposed that response modules are organized in a dimension-specific manner, but it is still an open question why SR-mappings should be organized in this manner. A full account of dimension change costs is outside the scope of the present study. However, it seems that a dimension-specific response bias could result from an adaptation to contingencies in the environment. Of note, in everyday life, changing the action (only) in response to a large change in the sensory input seems quite adaptive: For example, in repetitive tasks such a fruit-picking, attentionally selecting a fruit with slightly different features as the previous one (e.g., a yellower fruit when the previous one had been redder) would still often require the same action (e.g., picking the fruit). However, when attention is attracted to a salient stimulus from a different stimulus dimension (e.g., a moving beetle), the required action typically changes, too. Hence, a bias to change the response (or to inhibit the old response) upon changes of the stimulus dimension may result from adaptation to regularities in the environment, which dictate that executing the same response to stimuli from different dimensions will often be inappropriate.

Conclusion

The present study found dissociable effects of target feature changes and target dimension changes in visual search: While changes of the target feature interfered with visual selection, changes of the target dimension interfered with response selection. Of note, our EEG and fMRI results closely matched those of previous studies using a compound search task, indicating that feature and dimension changes affect search similarly across different paradigms. Yet, previous studies occasionally arrived at distinct conclusions, which highlight the importance of directly comparing feature and dimension changes in identical stimulus conditions and tasks. The present results support a visual selection account for target feature changes, and a response selection account for target dimension changes, thus providing new insights into the mechanisms of visual selection and response selection in visual search. Importantly, the present results also indicate the possibility of studying networks responsible for visual selection vs. response selection by systematically varying only the intertrial contingencies of the visual input.

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