Behavioral/Cognitive

**Improvement in Visual Search with Practice: Mapping Learning-Related Changes in Neurocognitive Stages of Processing**

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Practice can improve performance on visual search tasks; the neural mechanisms underlying such improvements, however, are not clear. Response time typically shortens with practice, but which components of the stimulus–response processing chain facilitate this behavioral change? Improved search performance could result from enhancements in various cognitive processing stages, including (1) sensory processing, (2) attentional allocation, (3) target discrimination, (4) motor–response preparation, and/or (5) response execution. We measured event-related potentials (ERPs) as human participants completed a five-day visual-search protocol in which they reported the orientation of a color popout target within an array of ellipses. We assessed changes in behavioral performance and in ERP components associated with various stages of processing. After practice, response time decreased in all participants (while accuracy remained consistent), and electrophysiological measures revealed modulation of several ERP components. First, amplitudes of the early sensory-evoked N1 component at 150 ms increased bilaterally, indicating enhanced visual sensory processing of the array. Second, the negative-polarity posterior–contralateral component (N2pc, 170–250 ms) was earlier and larger, demonstrating enhanced attentional orienting. Third, the amplitude of the sustained posterior contralateral negativity component (SPCN, 300–400 ms) decreased, indicating facilitated target discrimination. Finally, faster motor–response preparation and execution were observed after practice, as indicated by latency changes in both the stimulus-locked and response-locked lateralized readiness potentials (LRPs). These electrophysiological results delineate the functional plasticity in key mechanisms underlying visual search with high temporal resolution and illustrate how practice influences various cognitive and neural processing stages leading to enhanced behavioral performance.

**Key words:** attention; EEG; learning; LRP; N2pc; visual search

**Introduction**

Visual search, the process of detecting target items among distractors, is a vital cognitive ability central to many everyday human activities, as well as to societally critical job tasks such as detecting abnormalities in radiological images and screening airport luggage for contraband (for review, see Clark et al., 2012; Wetter, 2013). Successful search requires the execution of a cascade of fundamental cognitive processes, including sensory analysis of the scene, orienting of visual attention, working memory, target discrimination, and decision/response processes (for a review, see Eckstein, 2011; Nakayama and Martini, 2011). These cognitive faculties are supported by various underlying neural mechanisms ranging from low-level feature analyses to higher-level, goal-driven decision processes (Treisman and Gelade, 1980; Duncan and Humphreys, 1989; Corbetta and Shulman, 2002). Prior research has established that visual search can be improved through experience or practice (Sireteanu and Rettenbach, 1995; Sigman and Gilbert, 2000). Given the numerous neurocognitive stages involved in detecting, assessing, and responding to search stimuli, questions remain as to which processes are enhanced and in what relative combination. Several recent visual search studies have reported amplitude changes in certain scalp-recorded event-related potential (ERP) components after practice on complex conjunction search tasks (Hamane et al., 2011; An et al., 2012); however, the learning-related changes underlying training-induced behavioral improvement in the rapid, tightly timed, parallel processing involved in feature-popout search tasks are unclear.

Here, we investigated changes across the entire stimulus–response processing cascade that underlies popout visual search learning by leveraging the high temporal resolution of ERPs elicited while searching visual arrays containing rapidly processed feature-popout targets. Participants completed a five-day behavioral practice protocol (with electrophysiological activity re-
corded on days 1 and 5) to explore plasticity in the neural mechanisms underlying the expected practice-induced reduction in behavioral response time (Fig. 1A).

We assessed changes in four hallmark ERP components that reflect the cascade of cognitive processing stages from stimulus to response (Fig. 1B): (1) the posterior visual N1, a negative-polarity wave (latency ~150 ms) that reflects early sensory-evoked processing (Mangun and Hillyard, 1991); (2) the negative-polarity posterior–contralateral N2pc component (latency ~225 ms) associated with the shift of attention to a lateralized stimulus location (Luck and Hillyard, 1994a); (3) the sustained posterior–contralateral negativity (SPCN) component (latency 300–450 ms) or contralateral delay activity (CDA) that has been linked to maintenance and manipulation of information in visual working memory (Jolicoeur et al., 2008; Ikai et al., 2010) and/or to cognitive processing demands for target discrimination (Emrich et al., 2009; Luria and Vogel, 2011); and (4) the motor-related lateralized readiness potential (LRP) that reflects the initiation of a motor response (Coles, 1988).

By comparing the neural activity associated with these cognitive processes before and after the practice regimen, we aimed to elucidate neural plasticity underlying the expected improvements in visual search efficiency. Specifically, we assessed changes in the amplitude and/or latency of these ERP components to reveal how enhancements in sensory processing, attentional orienting, target discrimination, motor initiation, and/or motor execution contribute to improvement in visual search with practice.

Materials and Methods
Participants
Nineteen healthy individuals with normal or corrected-to-normal visual acuity and normal color vision were recruited and provided informed consent. All procedures were approved by the Duke University Medical Center Institutional Review Board. All individuals participated in a five-day visual search practice protocol for approximately 1 hour per day, over 5 consecutive days, beginning on a Monday and ending on the Friday of the same week. Before the start of the experiment on the first day, participants completed a brief (~5 min) session to become acquainted with the task. Behavioral performance (accuracy and response time) was recorded on all five days, and scalp-recorded EEG was measured on the first and last days of the protocol. Participants provided informed consent and were compensated at the rate of $15 per hour.

Data from two participants were excluded from the analyses because of poor behavioral performance (accuracy percentages more than 2 SDs below the group mean). Data from four additional participants were excluded because of producing suboptimal EEG data (excessive eye or muscle artifacts) on one or both of the EEG sessions. Data from the remaining 13 participants (ages 18–35 years, five female) were included in all analyses.

Figure 1. Hypothetical model indicating potential changes in behavior and ERP components in a visual search task after practice. A, Response time (RT) is expected to decrease after practice. B, Horizontal arrows indicate potential latency shifts in the N1, N2pc, and LRP components. Vertical arrows indicate potential amplitude changes in the P1/N1, N2pc, and SPCN components.

Figure 2. Sample stimulus display. The blue ellipses were distractors, the green ellipse was the relevant color popout target, and the red ellipse was the irrelevant color popout nontarget. Participants responded as to the orientation of the green target ellipse. In this example, a participant would respond by pressing the button corresponding to “horizontal.”

Search paradigm
Stimuli were programmed and presented using the Presentation software suite (Neurobehavioral Systems). During each of the five experimental sessions, participants completed a series of 14 blocks, each consisting of 140 trials and lasting ~4 min. Thus, each experimental session comprised 1960 trials and lasted ~56 min. Participants were seated without head restraint ~57 cm from the viewing monitor. A white fixation cross was presented at the center of the screen on a gray background and remained in place for the duration of each experimental block. Each trial consisted of a briefly presented (50 ms) circular array of 48 colored ellipses of which 46 were blue, 1 was red, and 1 was green (Fig. 2), with each stimulus subtending a visual angle of 1.36 × 0.91°. Thus, on each trial, there were two color popout stimuli in the array, a green ellipse (the target) and a red ellipse (an irrelevant nontarget popout distractor). These green and red ellipses could appear in one of 10 locations on the lower portion of the array on each trial and always appeared on opposite sides of each other.

Participants were instructed to report the orientation of the green target ellipse as quickly and accurately as possible. Responses were made using the left and right fingers on a game controller to indicate “vertical” or “horizontal” orientations, respectively. Participants were instructed to maintain central fixation during the stimulus presentation to minimize eye movements and preserve visual stimulation consistency. The 50 ms duration of the presented stimuli was sufficiently brief so as not to allow for a saccade to the target, and individual trials were separated by a stimulus-onset asynchrony that varied between 1300 and 1700 ms.
Behavioral data acquisition and analyses

Behavioral analyses. Behavioral responses were considered accurate if the participant responded with the correct orientation (vertical or horizontal) of the target stimulus between 200 and 1000 ms after the onset of the array. Response time was recorded as the time between the onset of the stimulus array and the button press for each correctly reported trial. Within-subject behavioral data acquisition and analyses were used to compare accuracy and response time over the course of practice.

EEG recording and analysis. On Sessions 1 and 5 of the experimental protocol, EEG data were recorded as participants performed the visual search task. Continuous EEG was recorded using a custom extended-coverage elastic cap with 64 equally spaced channels (Electro-Cap International), which covered the full head from slightly above the eyebrows to below the inion (Woldorff et al., 2002). Impedances of all channels were adjusted to below 5 kΩ; EEG was amplified within a frequency band of 0.016–100 Hz and digitized at a sampling rate of 500 Hz per channel (SynAmps; Neuroscan). Eye movements were monitored with vertical and horizontal EOG channels and a closed-circuit zoom-lens camera, and participants were given verbal feedback to encourage fixation on the central cross. Recordings took place in an electrically shielded, sound-attenuated, dimly lit experimental chamber.

For each participant, EEG data were selectively averaged to yield ERPs for the various conditions. All channels were re-referenced to the central cross. Recordings took place in an electrically shielded, sound-attenuated, dimly lit experimental chamber.

The participants’ task was to find the green ellipse, shift their spatial attention to this target covertly (i.e., without making an eye movement), and discriminate its orientation (a larger vertical or larger horizontal aspect ratio) with a manual response. The design of the task enabled the extraction of several prototypical ERP markers of the cognitive processes involved in visual search. First, by structuring the search arrays with both a task-relevant target popout (green among blue distractors) and a task-irrelevant nontarget popout (red among blue distractors), we were able to control for early sensory differences in the ERPs (Luck, 2005), while also eliciting robust N2pc and SPCN components. Additionally, the manual responses were executed with the index fingers of the left and right hands (left for vertical targets and right for horizontal targets), thereby allowing assessment of the LRP associated with motor-response initiation. Finally, the final response time was recorded for each trial.

Behavioral results. The response time (A) and accuracy values (B) are shown across the sessions. The response time decreased significantly over the course of practice, but there was no significant change in accuracy.

Changes in ERP components were assessed using two-tailed, paired t-tests or two-factor ANOVAs of the ERPs and/or ERP difference waves to compare amplitude and/or latency differences between Sessions 1 and 5.

Visual N1. To examine early sensory processing, EEG activity from parietal–occipital channels was used to calculate the amplitude and latency of the visual N1 component (Mangun and Hillyard, 1991). For this analysis, trials were divided according to whether the target appeared on the left or right side of the screen and activity in sites contralateral and ipsilateral to the target was assessed. Mean amplitude measures of the N1 for each participant were taken in a 25 ms latency window around the peak of the N1 (140–165 ms) observed in the across-subject grand-averaged ERP, and these values were compared between Sessions 1 and 5 to assess changes in basic sensory processing with practice. Peak latencies of the N1 were also measured for each participant and compared between Sessions 1 and 5 to assess for changes in speed of basic sensory processing.

N2pc. ERP difference waves reflecting activity associated with the attentional shift-related N2pc component were derived from parietal–occipital scalp sites, calculated as the difference between the activity in posterior electrodes contralateral minus those ipsilateral to the relevant popout target stimulus (Luck and Hillyard, 1994a). The resulting N2pc difference waves were compared between Sessions 1 and 5. The latencies of the peaks of the N2pc components were compared between Sessions 1 and 5 to determine whether the attentional shift to the target occurred sooner, relative to stimulus onset, after practice. These latencies were analyzed using both peak latency measures and onset latency measures. To capture the onset latencies, we calculated the fractional peak latency, the time at which the ERP waveform reached 50% of its peak amplitude (Luck, 2014). In addition, N2pc amplitudes were compared between Sessions 1 and 5 in the 40 ms latency window immediately surrounding the average peak latency collapsed over both sessions. Across both sessions, the average peak of the N2pc occurred at 228 ms (SD, 18 ms). Thus, amplitudes were assessed by comparing the mean amplitudes of the N2pc

Figure 3. Behavioral results. The response time (A) and accuracy values (B) are shown across the sessions. The response time decreased significantly over the course of practice, but there was no significant change in accuracy.
activity in the 40 ms window immediately surrounding the average peak latency.

SPCN. The SPCN (or CDA) component, which occurs after the N2pc, was also computed as a contralateral-minus-ipsilateral difference wave using the same calculation used for the N2pc, but examined in a later time window. The amplitudes of the SPCN component were analyzed in a broad time window after the N2pc component (340–480 ms after the stimulus array) and compared between Sessions 1 and 5 to assess changes in target-discrimination processes. Previous research has indicated that this component tends to become smaller for target-discrimination processes during search that are easier relative to those that are more taxing (Emrich et al., 2009; Luria and Vogel 2011).

LRP. Activity associated with the motor-related LRP component was calculated time-locked to both the stimulus array and the behavioral response. For both cases, this activity was calculated as the voltage difference between electrodes over the motor cortices contralateral versus ipsilateral to the hand used to execute the response on each trial (e.g., left for vertical orientation, right for horizontal orientation). For the LRP responses relative to the search array presentation, stimulus-locked activity over the motor cortex ipsilateral to the response hand was subtracted from the activity at the corresponding scalp site contralateral to the response hand, and the resulting LRP difference waves were compared between Sessions 1 and 5 to assess whether participants began to prepare motor responses more quickly after practice. These latencies were analyzed using both peak latency measures and onset latency measures (the latter using a 50% fractional peak latency calculation). The amplitudes of the LRP components between the two sessions were also compared, assessed in a 40 ms window around the grand-averaged peak of the component observed in each session. The response-locked LRP was derived at the same sites and using the same contralateral-minus-ipsilateral computation as the stimulus-locked LRP but was extracted such that it was time-locked to the behavioral response rather than to the stimulus. Baseline correction of the response-locked LRP waves was performed by subtracting the mean amplitude from 1.2 to 1 s before the motor response. Because trials with responses longer than 1000 ms were excluded, this approach ensured that there was no overlap between the baseline correction period and the stimulus-evoked ERPs. As with the stimulus-locked LRP, we used the fractional peak latency for statistical analyses of the response-locked activity.

Results
Behavioral results: response time and accuracy
As expected, participants responded more quickly after practice. There was a significant main effect of session on response time \(F(4,12) = 3.76, p = 0.008\) with an average decrease of 81.1 ms and a significant difference between Session 1 [546.7 ms (SD, 56.2)] and Session 5 [465.7 ms (SD, 50.8)]; \(t_{(12)} = 10.01, p < 0.001;\) Fig. 3A]. Improvement was observed in all participants, with the response time decreases ranging from 30.6 to 128.6 ms across the sample. Additionally, the average SD of individuals’ response times was 102.4 ms in Session 1 and 80.0 ms in Session 5 \(t_{(12)} = 8.70, p < 0.001\).

There were no differences in accuracy across the five sessions \(F(4,12) = 0.16, p = 0.96\) and no difference in accuracy in the direct comparison between Session 1 [88.2% (SD, 6.8%)] and Session 5 [90.2% (SD, 6.1%); \(t_{(12)} = 1.01, p = 0.33;\) Fig. 3B]; thus, participants maintained the same level of accuracy for the duration of practice. The fact that response time decreased significantly with no sacrifice in accuracy suggests that the improvement in response speed was not the result of a speed/accuracy tradeoff.

Electrophysiological markers
Early visual sensory processing: N1 effects
Mean amplitudes around the N1 peak (latency window, 140–165 ms) were significantly larger in Session 5 than in Session 1 for sites both contralateral \(t_{(12)} = 2.45, p = 0.03\) and ipsilateral \(t_{(12)} = 2.30, p = 0.04\) to the target (Fig. 4A; Table 1, amplitude). This overall amplitude increase in the N1 component bilaterally sug-

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**Table 1. Means and SDs of peak amplitudes and latencies of the peak of the N1 component**

<table>
<thead>
<tr>
<th></th>
<th>Session 1</th>
<th>Session 5</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Amplitude</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Contralateral to target</td>
<td>(-4.63 \mu V (2.16))</td>
<td>(-5.96 \mu V (2.90))</td>
<td>(t_{(12)} = 2.45, p = 0.03)</td>
</tr>
<tr>
<td>Ipsilateral to target</td>
<td>(-4.41 \mu V (2.11))</td>
<td>(-5.63 \mu V (2.85))</td>
<td>(t_{(12)} = 2.30, p = 0.04)</td>
</tr>
<tr>
<td><strong>Latency</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Contralateral to target</td>
<td>154.7 ms (13.7)</td>
<td>154.8 ms (12.2)</td>
<td>(t_{(12)} = 0.07, p = 0.95)</td>
</tr>
<tr>
<td>Ipsilateral to target</td>
<td>152.2 ms (13.7)</td>
<td>153.7 ms (12.0)</td>
<td>(t_{(12)} = 0.94, p = 0.36)</td>
</tr>
</tbody>
</table>

*Means and SDs of peak amplitudes of the sensory-evoked N1 component, collapsed across targets on the left and right sides of the display.*

*Means and SDs of latencies of the peak of the N1 component in response to targets on the left and right sides of the display.*
Figure 5. Effects on the N2pc and SPCN lateralized components, reflecting attentional orienting and target discrimination difficulty, respectively. A, ERP traces of activity used to calculate the difference waves for deriving the N2pc and SPCN components (contralateral vs ipsilateral to the target popout). B, Difference waves displaying N2pc and SPCN components in the posterior parietal–occipital regions of interest.

C, Distribution of N2pc-related activity over the scalp for Sessions 1 and 5.
D, Distribution of SPCN-related activity over the scalp for Sessions 1 and 5.
gests a generalized enhancement of neural responses to the stim-
ulus arrays with practice [also shown by the main effect of session
in the corresponding ANOVA ($F_{1,12} = 5.66, p = 0.035$)].

The analyses also showed that the N1 peak amplitudes (latency
window, 140–165 ms) were significantly larger in sites contralateral
to the target stimulus than in sites ipsilateral to the target stimulus
in both sessions ($t_{12} = 4.18, p < 0.002$). Given that the stimulus arrays
were controlled for left–right physical stimulus differences (a color
popout on each side), these effects were likely related to the analysis
including the early part of the contralaterality of the N2pc, which
began in the middle of the N1 latency range (see below). There was
also a trend for an interaction between laterality and session, but this
did not reach significance; thus, there was not a significant effect
of practice on the N1 laterality. No differences in the peak latency of
the N1 component were observed between any of the conditions (Table
1, latency).

**Allocation of attention: N2pc peak latency and amplitude**

After practice, the N2pc component peaked significantly sooner
(by ~19 ms, $t_{12} = 3.88, p = 0.002$; Fig. 5A–C; Table 2, peak
latency). Analysis of the onset latency measure [fractional peak
latency] also showed a significantly earlier onset with practice (by
9 ms, $t_{12} = 3.36, p = 0.005$). There was also a significant increase
in the amplitude of the peak of the N2pc component in the latency
window centered around the average time of the peak across subjects ($t_{12} = 2.42, p = 0.032$). Furthermore, there was a
relationship between individual participants’ initial N2pc peak
latencies and the amount of N2pc peak latency change with prac-
tice ($r = 0.72, p = 0.006$). Participants with initially later N2pc
latencies showed greater improvement after practice, suggesting
that there may have been more room to improve in those cases.

**Target discrimination: SPCN amplitude**

There was a significant decrease in the mean amplitude of the
SPCN component after practice [Session 1, $-0.29 \mu$V (SD, 0.9)];
Session 5, $0.03 \mu$V (SD, 0.9); $t_{12} = 4.05, p = 0.002$; Fig. 5A, B, D],
suggesting that practice facilitated target-discrimination pro-
cesses requiring retention and/or manipulation of information in
visual short-term memory.

**Motor-response preparation and execution: LRP onset latencies**

The onset of the stimulus-locked LRP component was signifi-
cantly earlier [fractional peak latency difference ~41 ms (SD, 20
ms)] in Session 5 than in Session 1 ($t_{12} = 7.4, p < 0.0001$; Fig. 6,
Table 3), reflecting earlier initiation of the motor response after
practice. This was further supported by the latency of the peak
amplitudes of the LRP component also being significantly earlier
[by ~47 ms (SD, 30 ms)] in Session 5 than in Session 1 ($t_{12} = 5.7,
p = 0.0001$). No difference was observed between the am-
plitude of the LRP component in Sessions 1 and 5. The onset of
the response-locked LRP was closer in time to the behavioral
response [fractional peak latency difference ~21 ms (SD, 19
ms)] in Session 5 compared with Session 1 ($t_{12} = 4.14, p =
0.0014$; Fig. 6), suggesting that practice led to more rapid mo-
tor execution after motor-response initiation. The amplitude of the LRP did not significantly change with practice.

**Summary of results**

The results from this study delineate learning and plasticity in key
phases of the neurocognitive processing chain associated with
behavioral improvements in visual search performance with prac-
tice. Over the course of five sessions of practice on a visual search
popout task, participants became significantly faster to detect and
discriminate targets, without any detriment in accuracy. The electro-
physiological measures of brain activity showed that this behavioral
performance improvement was accompanied by a significant bilat-
eral increase in the overall amplitude of the sensory-evoked visual
N1 ERP component to the array, an increase in amplitude and a
shortening in latency of the attention-shifting-sensitive N2pc, a sig-
nificant decrease in the amplitude of the SPCN reflecting reduced
target-discrimination resources demands, a significant quickening
of the onset latency of the LRP reflecting faster motor-response ini-
tiation, and a significant quickening of the time between the motor-
response initiation and response time.

**Discussion**

We aimed to elucidate how various stages of neurocognitive pro-
cessing involved in visual search are improved with practice on a
feature-popout search task. After practice on the task, we observed a
robust improvement in behavioral response times and changes in
several ERP indices that reveal the underlying neuroplasticity asso-
ciated with learning in this task. In the following sections, we discuss
the logic behind this experimental design and how the observed
practice effects demonstrate learning in the distinct cognitive pro-
cessing stages underlying visual search.

**Using ERPs to infer learning in visual search mechanisms**

ERPs provide a high-temporal-resolution measure of brain activity
that has been widely used to study the cognitive mechanisms under-
lying visual search abilities (Luck and Hillyard, 1994b; Jolicoeur
et al., 2009; Luck and Hillyard, 1994a; Hickey et al., 2009). In the current
study, we used a feature-popout search in which the target elements
possessed a feature that was absent from all distractors, thus captur-
ing attention and providing high-fidelity ERP components with
minimal trial-to-trial timing variability. The present design also re-
quired hand-specific manual responses and therefore enabled ex-
traction of the LRP activity reflecting motor response-related neural
responses, derived with both stimulus-locked and response-locked
analyses, thereby providing measures spanning the full cascade of
processes from stimulus processing to response execution. This ap-
proach differs from previous recent studies that have investigated
practice-related changes in visual search using conjunction search
stimuli (Hamane et al., 2011; An et al., 2012). Whereas those studies
have revealed some context-specific enhancements in the N2pc and
P3 components, the use of conjunction searches that require numer-
ous fixations make it difficult to infer the precise timing of brain
responses and only offer a limited view of the full cascade of mech-
isms that may change as a result of practice.

**Sensory processing**

After practice, we did not observe a change in the latency of the
N1 sensory component, indicating that speeding of basic visual
sensory processing did not contribute to the ultimate speeding of
response time. We did, however, observe a significant bilateral
increase in the amplitude of the N1 component after practice,
suggesting enhancement of overall early sensory responses to the
entire array with practice. A prior study did not find a robust

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**Table 2. Means and SDs of the amplitudes and latencies of the N2pc component**

<table>
<thead>
<tr>
<th></th>
<th>Session 1</th>
<th>Session 5</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amplitude$^a$</td>
<td>$-1.23 \mu$V (0.42)</td>
<td>$-1.44 \mu$V (0.45)</td>
<td>$t_{12} = 2.42, p = 0.032$</td>
</tr>
<tr>
<td>Peak latency$^b$</td>
<td>236 ms (18)</td>
<td>217 ms (13)</td>
<td>$t_{12} = 3.88, p = 0.002$</td>
</tr>
<tr>
<td>Onset latency</td>
<td>190 ms (18)</td>
<td>181 ms (15)</td>
<td>$t_{12} = 3.36, p = 0.006$</td>
</tr>
</tbody>
</table>

$^a$Means and SDs of the amplitudes of the N2pc component, collapsed across left and right targets (contralateral vs ipsilateral to the target popout).

$^b$Means and SDs of the latencies of the N2pc component, collapsed across left and right targets (contralateral vs ipsilateral to the target popout).

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change in N1 amplitude in response to practice in a conjunction search task (Hamame et al., 2011) and suggested that cortical reorganization at this early sensory processing stage may not have been necessary or beneficial for such a serial search task, whereas such early-processing plasticity did seem to be at play for our feature-singleton target-popout task. The larger N1s in Session 5 in the present study could be the result of directing more attention toward the incoming stimulus array after practice, as stronger attention to stimulus input has been shown to produce larger N1s (Luck et al., 1994a). We also observed a small degree of contralaterality of the early sensory-evoked N1 component that distinguished targets from nontargets (slightly larger contralateral to the target), but we did not find a significant training effect on this contralaterality.

### Table 3. Means and SDs of the onset and peak latencies of the LRP component

<table>
<thead>
<tr>
<th>Component</th>
<th>Session 1</th>
<th>Session 5</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stimulus-Locked</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset latency</td>
<td>362 ms (29)</td>
<td>321 ms (27)</td>
<td>t(_{12}) = 8.68, p &lt; 0.0001</td>
</tr>
<tr>
<td>Peak latency</td>
<td>443 ms (38)</td>
<td>395 ms (40)</td>
<td>t(_{12}) = 5.7, p = 0.0001</td>
</tr>
<tr>
<td>Response-Locked</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset latency</td>
<td>−131 ms (20)</td>
<td>−109 ms (18)</td>
<td>t(_{12}) = 4.14, p = 0.001</td>
</tr>
<tr>
<td>Peak latency</td>
<td>−60 ms (14)</td>
<td>−53 ms (19)</td>
<td>t(_{12}) = 1.1, p = n.s.</td>
</tr>
</tbody>
</table>

Allocation of attention

The N2pc is a parietal–occipital electrophysiological component (latency, 175–300 ms) that reflects a lateralized shifting and focusing of attention to a specified target item (Luck and Hillyard, 1994b).
Temporal changes in cognitive stages

The earliest temporal change after practice was observed in the N2pc (earlier in its onset by 9 ms, in its peak by 19 ms), reflecting a faster attentional shift to the target. An additional change in latency was apparent in the onset of the LRP, which occurred ~41 ms faster relative to stimulus onset after practice. Thus, earlier preparation for the motor response after attentional orienting contributed approximately ~20–30 ms to the overall improvement in response time, facilitation that likely suggests a more efficient target discrimination process after practice, as reflected by the reduction in the SPCN. Accordingly, the latency shifts observed in the N2pc and the LRP together account for ~41 of the ~81 ms change in response time, suggesting that additional speeding of processing occurred between the initiation and execution of the motor response. Finally, increased efficiency in response execution (as reflected by the reduction in time between the onset of the LRP in the response-locked LRP and the actual motor output, measured by 50% fractional peak latency) specifically accounted for an additional 20–30 ms of the total observed behavioral improvement.

Conclusions

Our primary goal was to determine which cognitive processes underlying visual search are enhanced with practice and to delineate their relative contributions to improved behavioral performance. In parallel with a marked decrease in behavioral response time with practice, we observed a number of changes in the underlying neural activity associated with specific cognitive mechanisms leading up to the behavioral response, namely, enhanced early sensory processing to the visual search array, enhanced and earlier attention orienting to the popout target item, decreased need of resources required for target discrimination, more rapid initiation of motor-response preparation, and more rapid execution of the motor response after that initiation.

Visual search is a complex but critical cognitive function that requires a cascade of component processes to be performed successfully and effectively. The present findings elucidate specific practice-induced changes in the component neurocognitive stages underlying visual search and offer a principled method for probing the neural mechanisms underlying learning in this essential cognitive ability.

References

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