

1 **RUNNING HEAD: Complete transfer between component and pattern motion**

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4 **Disentangling locus of perceptual learning in the visual**
5 **hierarchy of motion processing**

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32 **ABSTRACT**

33 Visual perceptual learning (VPL) can lead to long-lasting perceptual improvements.
34 While the efficacy of VPL is well established, there is still a considerable debate about
35 what mechanisms underlie the effects of VPL. Much of this debate concentrates on where
36 along the visual processing hierarchy behaviorally relevant plasticity takes place. Here,
37 we aimed to tackle this question in context of motion processing, a domain where links
38 between behavior and processing hierarchy are well established. Specifically, we took
39 advantage of an established transition from component-dependent representations at the
40 earliest level to pattern-dependent representations at the middle-level of cortical motion
41 processing. We trained two groups of participants on the same motion direction
42 identification task using either grating or plaid stimuli. A set of pre- and post-training
43 tests was used to determine the degree of learning specificity and generalizability. This
44 approach allowed us to disentangle contributions from both low- and mid-level motion
45 processing, as well as high-level cognitive changes. We observed a complete bi-
46 directional transfer of learning between component and pattern stimuli as long as they
47 shared the same apparent motion direction. This result indicates learning-induced
48 plasticity at intermediate levels of motion processing. Moreover, we found that motion
49 VPL is specific to the trained stimulus direction, speed, size, and contrast, highlighting
50 the pivotal role of basic visual features in VPL, and diminishing the possibility of non-
51 sensory decision-level enhancements. Taken together, our study psychophysically
52 examined a variety of factors mediating motion VPL, and demonstrated that motion VPL
53 most likely alters visual computation in the middle stage of motion processing.

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56 INTRODUCTION

57 A large body of evidence has shown that the human visual system can gain long-lasting
58 perceptual improvements following several sessions of perceptual training. This
59 phenomenon, called visual perceptual learning (VPL), has been an active area of research
60 because VPL is a remarkable demonstration that human vision can remain plastic even in
61 adulthood ^{1,2}. Numerous studies have revealed training-induced perceptual improvements
62 on a wide range of visual tasks, including low-level contrast and orientation
63 discrimination tasks ^{3,4,5,6}, mid-level motion and form tasks ^{7,8,9} and even high-level
64 object and face recognition tasks ^{10,11}.

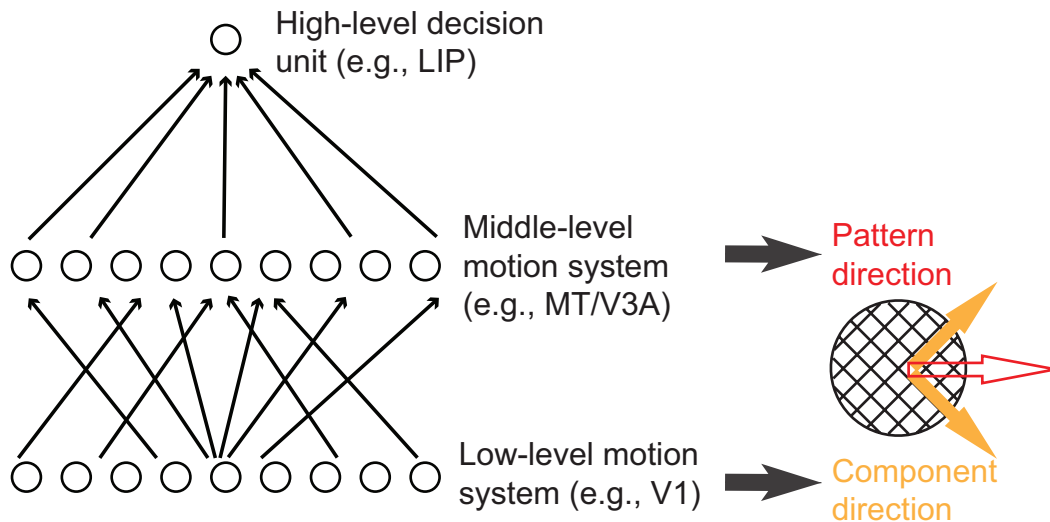
65 While the robustness of learning effects is well established, debate persists with
66 respect to the mechanisms underlying VPL. Early psychophysical work found that
67 learning effects are usually confined to the trained parameters ^{6,12}. Such strong specificity
68 suggests that VPL most likely takes place within low-level visual areas (e.g., V1 or V2)
69 since neurons therein exhibit narrow ranges of spatial and feature selectivity (e.g.,
70 orientation, motion direction). Recent evidence, however, challenges this idea by
71 revealing an increasing number of cases where the transfer of VPL is viable to novel
72 stimulus conditions and tasks ^{13,14}. This is consistent with an involvement of higher-level
73 visual areas, wherein neurons usually respond to larger spatial areas and more complex
74 stimulus features. Some studies even suggest the contributions from the brain areas that
75 process non-sensory attributes. For instance, perceptual learning might manifest as the
76 change of decision variables encoded in the prefrontal cortex ¹⁵. Alternatively, perceptual
77 learning might facilitate encoding of abstract concepts representing basic visual features
78 (e.g., orientation and contrast) ¹⁶ or lead to a better set of task-specific rules ¹⁷. Given that
79 these theories postulate changes beyond canonical sensory mechanisms, we refer to them
80 as ‘non-sensory’ learning processes.

81 The task of linking VPL to specific brain areas is complicated by the complex
82 functional specializations of the brain. The brain includes multiple brain regions that are
83 organized into a coarse, but richly interconnected hierarchy ^{18,19}. Even a simple
84 perceptual choice likely arises from the interplay among multiple brain regions. One
85 strategy is to take advantage of visual processes where links between behavior and neural
86 structures are well established. Here, we focus on VPL in context of motion perception, a

87 perceptual domain where we have a relatively advanced understanding of different
88 processing stages [20](#). In primates, neurons selective to motion direction first occur in the
89 earliest cortical areas V1 and V2 [21](#). However, conscious motion perception is most
90 closely linked to intermediate visual areas, such as MT and V3A. These areas contain a
91 large portion of neurons showing strong preferential responses to different motion
92 directions [22,23,24,25](#). In addition, perceptual decisions based on motion stimuli have been
93 linked to several higher-level brain areas (e.g., lateral intraparietal cortex (LIP) and
94 prefrontal cortex). These areas are often ascribed as “evidence accumulators” that
95 integrate sensory information provided by the upstream motion processing units in order
96 to form perceptual decisions and guide visual behaviors [26,27](#) (but see ref. [28](#)). Finally, non-
97 sensory attributes, such as task rules and decision strategies, encoded in high-level
98 cognitive areas, can also mediate performance in motion perception tasks [29](#). This
99 complex hierarchy can be operationalized as a symbolic three-layer network (Figure 1).
100 This network consists of a low-level (e.g., V1/V2), a middle level (e.g., MT/V3A) and a
101 high-level (e.g., LIP, prefrontal cortex) processing stage.

102 In contrast with the established understanding of visual motion processing stages,
103 their role in human VPL is largely unknown. To address this question, we took advantage
104 of an established transition from component-dependent representations at the earliest
105 level to pattern-dependent representations in the middle-level of cortical motion
106 processing [30,31](#). A plaid stimulus composed of two obliquely moving gratings (Figure 1)
107 is generally perceived as a rigid object moving horizontally [32](#). While many MT neurons
108 faithfully respond to the perceived motion direction in moving plaids, neurons in V1
109 primarily respond to the directions of two component gratings [30,31](#). This dissociation
110 allows us to psychophysically infer the main locus of the behaviorally related plasticity
111 induced by motion VPL. If learning effects are specific to the trained component motion,
112 irrespective of the perceived pattern motion, it would indicate component-dependent
113 learning predominantly at the lowest levels of motion processing. Conversely, if learning
114 effects are specific to the perceived pattern motion, it would point toward pattern-
115 dependent learning at middle-levels of motion processing. If this learning still retains
116 some sensory-level specificity (e.g., speed, size and velocity), we can conclude that non-

117 sensory cognitive processes are not the major drivers of the observed behavioral
118 improvement.



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120 Figure 1. A simplified hierarchy of visual motion processing with three
121 hierarchical stages ²⁰. Neurons in the low-level motion system respond
122 best to component directions of plaid stimuli (full orange arrows).
123 Neurons in the middle-level motion system respond selectively to the
124 perceived pattern motion direction (empty red arrow). In this and all
125 subsequent figures, empty arrows indicate faster perceived speed
126 associated with plaid motion. The third stage involves complex sensory
127 and non-sensory high-level cognitive processes.

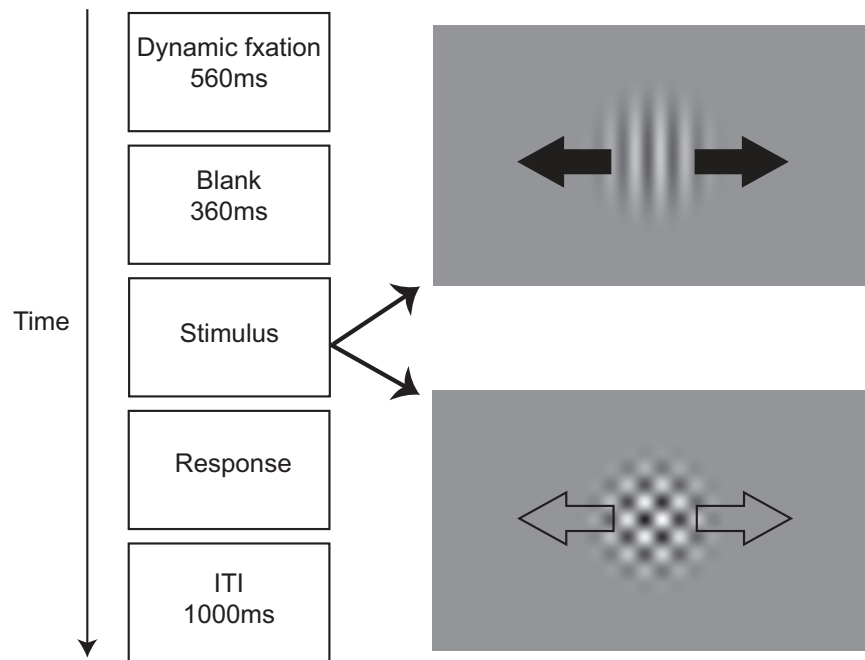
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129 **METHODS AND EXPERIMENTAL PROCEDURES**

130 **Participants and apparatus**

131 Fourteen undergraduate students from University of Rochester (18 to 22 years old, 5
132 males and 9 females) took part in this study. All participants had normal or corrected-to-
133 normal vision. The Research Subjects Review Board at the University of Rochester
134 approved experimental protocols and all participants provided written consent forms.
135 Stimuli were generated by Matlab Psychtoolbox ³³ and presented using customized
136 digital light processing (DLP) projector (DepthQ WXGA 360 driven by a NVIDIA
137 Quadro FX 4800 at 1280 × 720 resolution). The projector frame rate was 360 Hz,
138 resulting in discrete 2.78-ms frames. DLP projectors are natively linear, and this was
139 verified with a Minolta LS-110 photometer. Viewing distance was 61.5 inches, with a
140 projected image of 46.74 × 25 inches.

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143 Figure 2. Task illustration showing trial structure used for all training, pre-
144 and post-test conditions. Participants viewed a moving stimulus that was
145 either a grating or a plaid (arrows are for illustration purposes only).
146 Stimulus duration varied on each trial, as determined by two interleaved
147 staircases. Participants indicated the perceived stimulus direction via
148 button press (e.g., left vs. right in this case).

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150 **Stimulus and task settings**

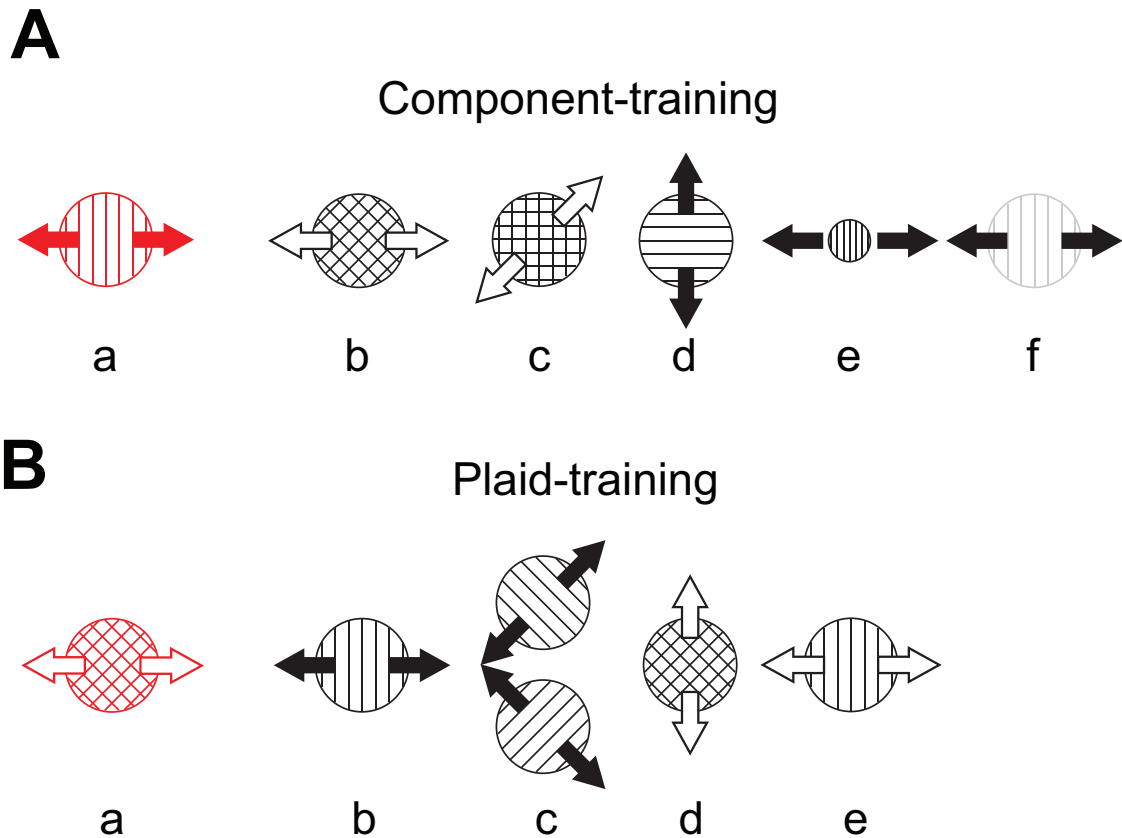
151 Participants were randomly assigned into two groups – one group trained on component
152 motion (grating; N = 8) and another group trained on pattern motion stimuli (plaid; N =
153 6). All participants were tested and trained on a two-alternative forced choice motion
154 direction identification task (Figure 2), reporting the perceived stimulus motion direction
155 via key press. Auditory feedback was provided after each trial during the training phase
156 but not at pre-/post-test (to minimize learning effects in pre-/post-test). To facilitate
157 fixation, we used the following fixation sequence (Figure 2): a fixation circle (0.8°
158 radius) appeared after each key press response and, the circle shrank to 0.13° over 200
159 ms, remained at that size for 360 ms, and then disappeared 360 ms before stimulus onset.
160 We found in our previous work that this dynamic fixation sequence was very effective in
161 guiding eye gaze to the center of the screen before the stimulus onset ³⁴. The inter-trial
162 interval was 1000 ms.

163 As detailed below, the two training groups used partially overlapping sets of pre-
164 and post-test conditions. We selected this design to limit pre- and post-test sessions to
165 only the most diagnostic test conditions for each group. This allowed us to test the
166 bidirectional transfer between component and pattern motion, as well as the dependency
167 of learning transfer on several key low-level stimulus features.

168 In the component-training group, the training stimulus was a grating (contrast =
169 50%, drift speed = $4^\circ/\text{s}$, radius = 8° , 2D raised cosine spatial envelope; spatial frequency
170 = 1 cycle/ $^\circ$; Figure 3Aa). Training motion directions were either left/right or up/down,
171 counterbalanced across participants. Motion directions for other stimulus conditions were
172 adjusted according to the directions of trained stimuli. During the pre- and post-test,
173 temporal duration thresholds (defined by the full-width at half-height of a hybrid between
174 a Gaussian and a trapezoidal temporal envelope; see [35](#) for details) were measured across
175 another five stimulus conditions: (1) a plaid stimulus moving in the trained directions
176 (Figure 3Ab); (2) a plaid stimulus containing the trained component and moving 45°
177 away from the trained direction (Figure 3Ac); (3-5) moving gratings that matched the
178 trained grating except that they differed in (3) direction and orientation (orthogonal to the
179 trained direction; Figure 3Ad), (4) stimulus size (radius = 1° , Figure 3Ae), and (5)
180 contrast (contrast = 2%, Figure 3Af).

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Figure 3. Pre- and post-training stimuli for (A) the component-training group and (B) the plaid-training group. The red icons show the training stimulus for each group. These conventions are kept in subsequent figures. With the exception of Be, the speed of all grating stimuli was $4^\circ/s$ (marked by solid arrows). The plaid component speed was also $4^\circ/s$, which resulted in the apparent plaid speed of $5.66^\circ/s$ (marked by empty arrows). To assess the effect of stimulus speed on transfer of learning, we also included a grating whose speed matched the plaid speed of $5.66^\circ/s$ (Be, empty arrows). Although all stimulus conditions were conducted together, we analyze and present data into two batches: bidirectional transfer between component and pattern motion (Figure 5) and transfer to other stimulus features (Figure 6).

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For the plaid-training group, the plaid stimuli consisted of two orthogonal component gratings (component contrast = 50%, size = 8° , 2D raised cosine spatial envelope; component spatial frequency = 1 cycle/ $^\circ$; Figure 3Ba). Component drift speed was $4^\circ/s$, which resulted in the plaid velocity of $5.66^\circ/s$. Training motion directions were

201 either left/right or up/down, counterbalanced across participants. In addition to the trained
202 condition, duration thresholds were measured for five additional pre- and post-test
203 stimulus conditions: (1) a moving grating with the same apparent direction and speed as
204 the trained plaid stimulus (Figure 3Bb); (2, 3) two component gratings that constituted
205 the trained plaid stimulus (i.e., gratings with direction $\pm 45^\circ$ away from the trained
206 directions; Figure 3Bc. Note that these data were collected in two separate blocks, each
207 testing one motion direction axis, and subsequently averaged to get a single threshold
208 estimate); (4) a plaid stimulus moving to the untrained directions, but comprised of same
209 static component features (Figure 3Bd); (5) a grating moving in the trained directions
210 (left/right) but with the original plaid apparent speed (speed = $5.66^\circ/\text{s}$, Figure 3Be).

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212 **Experimental procedures and Data analysis**

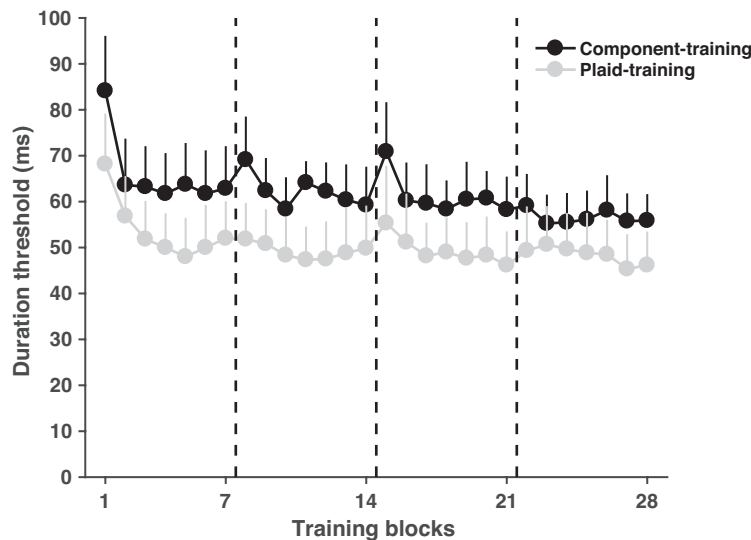
213 Pre- and post-test consisted of six randomly ordered blocks corresponding to different
214 stimulus conditions (the trained stimulus, plus 5 additional stimulus conditions, as
215 described above). In each block, stimulus durations were controlled by two 80-trial
216 interleaved staircases (a 2-down-1-up staircase and a 3-down-1-up staircase), yielding
217 160 trials for each threshold estimate. The initial starting durations for two staircases
218 were 100 ms and 110 ms, respectively. Pre- and post-test measurements were conducted
219 on day 2 and day 7, respectively. On day 1, each participant completed a practice phase
220 that was identical to the pre- and post-test battery, except that each block consisted of
221 only 60 trials. The purpose of this practice day was to help stabilize pre-test
222 measurements. The perceptual training lasted four days (days 3-6). On each day,
223 participants completed seven 100-trial blocks, resulting in a total of 28 training blocks.
224 For the first training block on the first training day (day 3), the initial starting durations
225 for the two staircases were 100 ms and 110 ms. For all subsequent training blocks, the
226 initial stimulus durations were the durations in the final trials of two staircases in the
227 previous training block. All participants completed these seven experimental sessions
228 within 14 days.

229 To estimate duration thresholds for each pre- and post-test condition, we fit
230 Weibull psychometric functions to 160 trials of raw data using the maximum likelihood

231 method, estimating the thresholds at 82% correct. The amount of learning in each
232 condition was estimated by computing percent of improvement (PI):

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$$PI = \frac{threshold_{pre} - threshold_{post}}{threshold_{pre}} * 100\% \quad (1)$$

234 where $threshold_{pre}$ and $threshold_{post}$ indicate duration thresholds for the corresponding
235 pre- and post-test stimulus conditions. We used paired t-tests for comparisons of pre- and
236 post-test thresholds and for comparison of PI across stimulus conditions. One-sample t-
237 tests were used for assessing the statistical significance of PI against the null hypothesis
238 of 0% PI. All t-tests were two-tailed and performed using Matlab Statistical and Machine
239 Learning Toolbox.



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241 Figure 4. Learning curves for the component- (black) and the plaid-
242 training (gray) group. Data are thresholds for 28 training blocks, tested
243 over 4 days of training. Vertical dashed lines separate data for four
244 training days. Note that the plaid-training group showed lower duration
245 thresholds. This is expected given the faster apparent speed of plaid
246 stimuli and known effects of stimulus speed on temporal duration
247 thresholds ³⁶. Error bars are SEM across subjects.

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249 RESULTS

250 Effective perceptual learning for both component and plaid stimuli

251 We first examined whether our training procedure was sufficient to result in perceptual
252 improvement. Here, for each group, we compared pre- and post-test thresholds for the
253 trained stimulus condition. The results revealed significant improvements in thresholds

254 for both the component- and the plaid-training group (Figure 5E; $t(7) = 2.79$, $p = 0.0268$
255 and $(5) = 6.28$, $p = 0.0015$, respectively). We also computed percent of improvement (PI,
256 see Equation 1), and found significantly positive PIs for both groups (Figure 5F; $t(7) =$
257 5.06 , $p = 0.0015$; $t(5) = 12.04$, $p = 6.97 \times 10^{-6}$), with each group showing about a 20%
258 improvement in performance.

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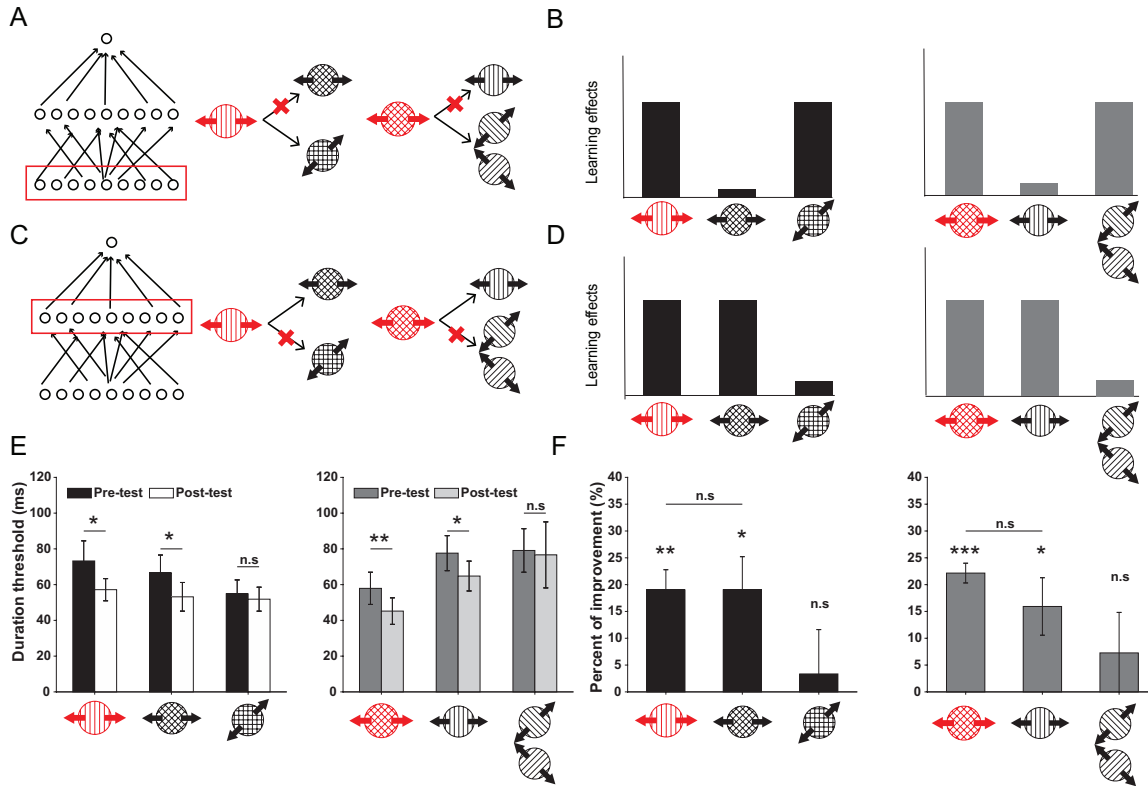
260 **Bidirectional transfer of learning between component and plaid motions**

261 The main focus of this paper is to examine the transfer of perceptual learning to a range
262 of diagnostic stimulus conditions. A two-stage criterion was used to assess transfer of
263 learning. First, we concluded that learning transfers to a stimulus condition if the pre-
264 /post-test difference on this condition was statistically significant. If a stimulus condition
265 passed this first test, then we compared its PI to the corresponding trained condition (i.e.,
266 either trained component or trained plaid). If the transfer PI was significantly smaller than
267 the trained PI, the result was described as a “partial transfer”. Alternatively, if the PI for a
268 transfer condition was not statistically smaller than the PI for its corresponding trained
269 condition, we referred to it as “complete transfer”, according to an established convention
270 in VPL research [13,16,17](#).

271 The key aim of this study was to determine whether perceptual training leads to
272 plasticity within low-level component-dependent motion processing or middle-level
273 pattern-dependent motion processing. To be precise, component-dependent plasticity
274 predicts that training on a component motion stimulus should only transfer to the plaid
275 composed of the trained component gratings, and that training on a plaid stimulus should
276 only transfer to its two constituent components (Figure 5A-B). On the contrary, pattern-
277 dependent plasticity predicts that training on a component motion stimulus or on a plaid
278 motion stimulus that moves in the same directions should mutually transfer to each other
279 (Figure 5C-D).

280 Our results were consistent with plasticity in pattern-dependent mechanisms. First,
281 perceptual training on a component grating significantly reduced the duration thresholds
282 on the plaid that moved in the same apparent direction as the trained grating (Figure 5E
283 left panel, pre-/post-test, $t(7) = 2.88$, $p = 0.0237$; Figure 5F left panel, PI, $t(7) = 3.08$, $p =$
284 0.0178). More importantly, the PI was statistically equivalent to the PI on the trained

285 grating (Figure 5F left panel; $t(7) = 0.002$, $p = 0.999$). Consistently, perceptual training
286 on a plaid stimulus also transferred to the component grating that moved in the same
287 apparent direction (Figure 5E right panel, pre-/post-test, $t(5) = 3.336$, $p = 0.0207$; Figure
288 5F right panel, PI, $t(5) = 2.971$, $p = 0.0311$). Also, the PI on the untrained component was
289 not statistically different from the PT on the original trained plaid (Figure 5F right panel,
290 PI, $t(5) = 1.29$, $p = 0.2533$). The bidirectional transfer between the component and the
291 plaid stimuli that moved to the same directions suggest that perceptual training most
292 likely alters the computation in the visual units that process the pattern motion direction.
293 Moreover, training effects on a component did not significantly transfer to a plaid that
294 included the trained component, but moved in a different direction (Figure 5E left panel,
295 pre-/post-test, $t(7) = 0.784$, $p = 0.4586$; Figure 5F left panel, PI, $t(7) = 0.405$, $p = 0.6978$).
296 Plaid training also did not improve the performance on its two constituent components
297 (Figure 5E right panel, pre-/post-test, $t(5) = 0.305$, $p = 0.7709$; Figure 5F right panel, PI,
298 $t(5) = 0.963$, $p = 0.3797$). Taken together, these findings suggest that pattern-dependent
299 learning at the middle-level motion system, rather than component-dependent learning at
300 the low-level motion system, plays a pivotal role in mediating learning transfer of motion.
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Figure 5. Schematic illustrations (A, C), predictions (B, D) and empirical results (E-F) for component-dependent and pattern-dependent VPL. **A.** The component-dependent VPL takes place at the lowest level of motion processing, as indicated by the red rectangle. Here, training on a component stimulus should only transfer to the plaid stimulus that comprises the trained component. Moreover, training on a plaid stimulus should only transfer to its two constituent components. **B.** Learning effects as predicted by component-dependent learning in panel A. **C-D.** Illustrations of the pattern-dependent perceptual learning and its predicted learning effects, following conventions in panels A and B. Here, plasticity takes place at the middle stage of motion processing. (E) Duration thresholds at pre-/post-test across stimulus conditions in the component (left panel) and the plaid training (right panel), respectively. (F) Learning effects quantified as percent of improvement (PI%) across stimulus conditions and training regimes. The overall pattern mimics the predictions in (D), indicating that plasticity likely occurs at the middle-level of motion analysis. For all subplots, error bars denote ± 1 SEM across subjects. Significance symbol conventions are *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; n.s.: non-significant. Same definitions of error bars and symbol conventions are kept for all figures in this paper.

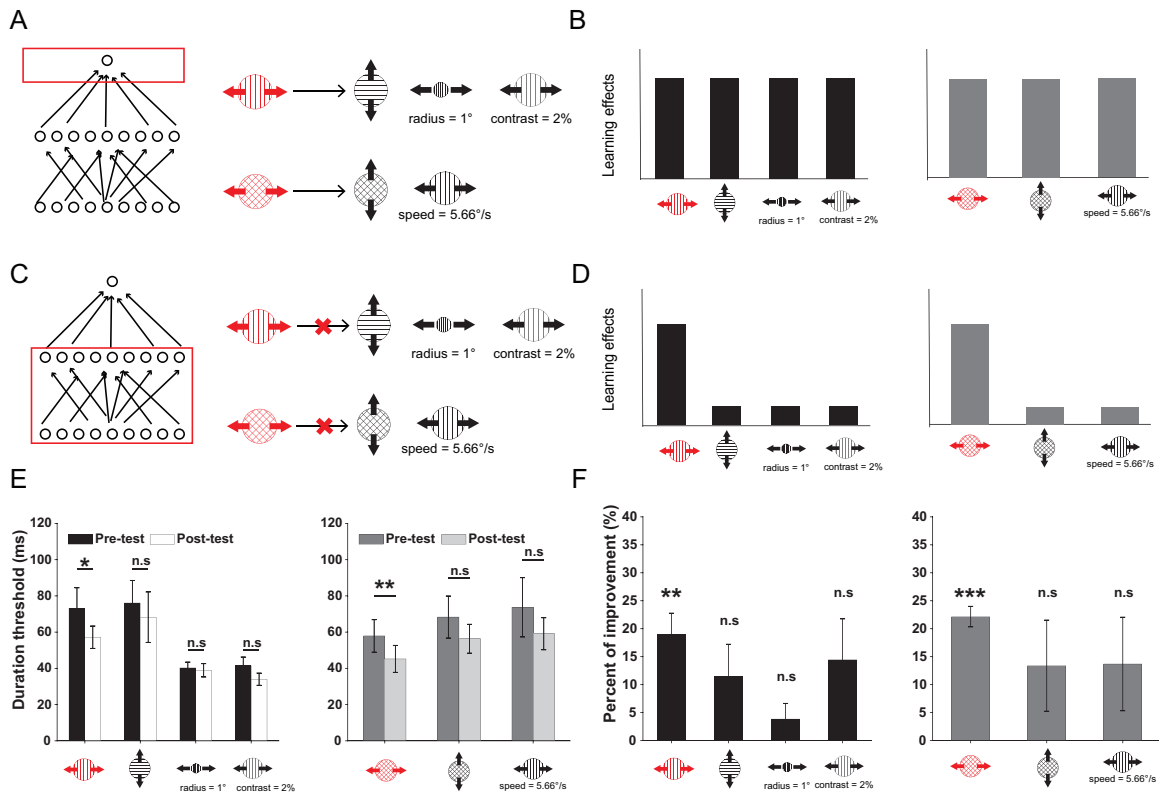
327 **Specificities to direction, speed, size, and contrast**

328 We have thus far focused on experimentally disentangling component-dependent from
329 pattern-dependent VPL, with the results arguing against low-level component-dependent
330 VPL. What remains unclear, however, is whether the perceptual training led to
331 enhancements in the processing of sensory features or high-level non-sensory attributes.
332 For instance, participants might learn motion directions as abstract concepts ¹⁶ or be more
333 familiar with the general task statistics (e.g., stimulus timing, stimulus-response
334 association ¹⁷). In this case, plasticity takes place in higher brain hierarchy that is
335 independent of the sensory processing. To further delineate the plasticity in the sensory
336 (Figure 6A-B) or the non-sensory processing (Figure 6C-D), we examined the tolerance
337 of our training across several other forms of stimulus variations, i.e., direction, speed,
338 size, and contrast. The prediction is that if the plasticity is largely limited to sensory
339 processing, learning should be confined to the trained stimuli; otherwise learning effects
340 will transfer irrespective of the variations in other stimulus features.

341 The results indicated a notable specificity to stimulus variations. In the
342 component-training group, we did not find significant transfer for trained and test stimuli
343 that differed in motion directions (Figure 6E left panel, pre-/post-test, $t(7) = 1.886$, $p =$
344 0.101 ; Figure 6F left panel, PI, $t(7) = 2.016$, $p = 0.084$). We also found no significant
345 transfer to test stimuli that have smaller size (Figure 6E left panel, pre-/post-test, $t(7) =$
346 1.308 , $p = 0.232$; Figure 6F left panel, PI, $t(7) = 1.376$, $p = 0.211$) or lower contrast
347 (Figure 6E left panel, pre-/post-test, $t(7) = 2.187$, $p = 0.065$; Figure 6F left panel, PI, $t(7)$
348 $= 1.971$, $p = 0.089$).

349 Similarly, if component motion directions were switched such that the resulting
350 plaid moves in an orthogonal direction, transfer effects in the plaid-training group were
351 not statistically evident (Figure 6E right panel, pre-/post-test, $t(5) = 1.268$, $p = 0.261$;
352 Figure 6F right panel, PI, $t(5) = 1.645$, $p = 0.161$). We also investigated how changing
353 stimulus speed affects learning transfer. When the grating speed was increased to match
354 the apparent speed of the trained plaid, the transfer effect was not significant (Figure 6E
355 right panel, pre-/post-test, $t(5) = 1.257$, $p = 0.265$; Figure 6F right panel, PI, $t(5) = 1.635$,
356 $p = 0.163$).

357 Taken together, we find that motion VPL is specific to stimulus direction, speed,
 358 size, and contrast. These results demonstrate that our training has strong susceptibilities
 359 to variations in basic visual features. Such strong dependencies indicate that a broadly
 360 tuned non-sensory learning mechanism unlikely plays an important role in observed
 361 learning because it predicts a broad transfer over variations in low-level stimulus features.
 362 Note that we cannot completely eliminate the possibility of changes in sensory readout
 363 mechanisms since, theoretically, a refined readout mechanism can be sensitive to changes
 364 in sensory features [37,38](#). Nonetheless, these results suggest the pivotal roles of basic
 365 stimulus features in perceptual learning of motion.
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Figure 6. Specificity of motion VPL to basic sensory features. **A-B**. Illustrations and predictions of the plasticity at the highest-level stage (e.g., PFC) in the three-layer network. This mechanism predicts that training on a component or a plaid stimulus should be generalizable regardless of the variations in low-level visual features, such as direction, speed, size, and contrast. **C-D** Illustrations and predictions akin to (A-B), expect that the plasticity occurs within the general sensory representation stage. This scheme predicts that training on a component or a plaid stimulus should

377 exhibit minimal transfer to the stimuli that differ in basic visual features. (E)
378 Duration thresholds at pre-/post-test across stimulus conditions in two
379 training groups. (F) Empirical learning effects, quantified as percent of
380 improvement (PI%), across stimuli and training groups. The transfer pattern
381 of learning is more consistent with predictions in (D). No significant transfer
382 in all other stimulus conditions is noted, implying the plasticity within the
383 sensory representation level as shown in (C).
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385 **DISCUSSION**

386 Elucidating where in the visual processing hierarchy plasticity associated with VPL takes
387 place has been a key question in perceptual learning research over the past decades. Here,
388 we addressed this question in the domain of motion perception. We trained participants to
389 identify motion directions of either component motion (a drifting grating) or pattern
390 motion (a drifting plaid), and assessed transfer of learning to a variety of carefully
391 controlled stimulus conditions. The bidirectional transfer of learning between component
392 and pattern motion provides evidence that learning effects most likely take place at the
393 middle-levels of processing where component motions are combined into plaid percepts,
394 and, at the same time, rules out plasticity at the low-levels where complex motions are
395 represented as components. In addition, we also observed specificities to the trained
396 direction, speed, stimulus size, and contrast. These results are in line with the previous
397 findings that VPL is generally vulnerable to the variations in basic feature dimensions
398 and argue against plasticity in high-level brain areas that represent non-sensory cognitive
399 factors, such as general task statistics and decision rules [15,16,17](#).

400 Our results are of significance for understanding mechanisms underlying motion
401 perception. As one of the key research topics in vision science, dissociable functional
402 roles of the low-level and the middle-level motion system have been well documented
403 [22,39,40](#). The seminal paper by [Adelson and Movshon](#) ³² documented how moving plaid
404 percepts can arise from component gratings. Subsequent neurophysiological work
405 discovered distinct tuning properties of individual neurons in V1 and MT with
406 preferences toward component and plaid representations, respectively ³⁰. These findings
407 were generalized to humans. [Huk and Heeger](#) ⁴¹ reported robust fMRI adaptation to
408 pattern motion in the human motion-sensitive area hMT+. Thus, the phenomenon of

409 component and pattern motion serves as a good benchmark for studying visual hierarchy
410 of motion processing.

411 Although we have a good understanding of visual motion processing hierarchy,
412 we know little about the roles different stages play in VPL. We address this question by
413 showing that training on component or pattern motion bi-directionally transfers to each
414 other if the two stimuli share the same apparent motion direction. These results suggest
415 that, when a plaid motion stimulus is being learned, learning signals might preferentially
416 refine the pattern-selective units that respond to the apparent motion direction, but not the
417 component sensitive units. While there have been many behavioral studies of motion
418 VPL, to our knowledge, no studies employed an experimental design that allowed
419 distinguishing between plasticity at low and at the middle levels of motion processing.
420 For instance, VPL studies typically relied on random-dot-kinematogram stimuli or
421 trained subjects on fine direction discrimination tasks [7,42,43](#). Studies that used gratings
422 only tested contrast thresholds for coarse motion direction judgments [44](#).

423 Our study also constrains theoretical models of VPL. Two distinct computational
424 frameworks of VPL have emerged so far, where learning either improves the quality of
425 sensory encoding or optimizes high-level readout and decision mechanism that can in
426 turn promote perceptual sensitivity. Empirical evidence, however, is highly contentious.
427 Early psychophysical studies on motion VPL demonstrated the considerable specificity to
428 the trained direction [7,8](#), implying the plasticity among direction-selective units. However,
429 specificities in motion VPL have also been shown to be mediated by other factors, such
430 as task difficulty [45,46](#), exposure to other directions [47](#), external noise [44](#). This debate in
431 VPL psychophysics is mirrored by a similar debate with respect to the neural substrates
432 of VPL. For example, after training monkeys on a motion direction decision task, [Law](#)
433 [and Gold](#) [27](#) found pronounced behaviorally relevant changes in neural responses in area
434 LIP, but minimal changes in neural activities in area MT. This study advocates a
435 mechanism beyond the sensory-representation level, where training results in a more
436 efficient extraction of useful sensory information rather than in an enhancement of
437 sensory representations per se. In contrast, recent fMRI studies found that motion VPL
438 refines the cortical tuning of the human MT, emphasizing the pivotal role of enhancement
439 at sensory-representation level [48,49](#). Notably, the mechanistic role of high-level cognitive

440 influences in sensory processing is still largely unknown. Previous studies have suggested
441 at least two broad categories, mechanisms that are sensory (e.g., selective readout) and
442 those that are non-sensory (e.g., conceptual learning, rule-based learning). While
443 disentangling between these higher level processes is beyond the scope of this paper, the
444 observed specificity to basic stimulus features argues against non-sensory cognitive
445 factors.

446 What are the possible neural underpinnings of the observed empirical findings in
447 the present work? We surmise that several mechanisms may coexist and interact. First,
448 because training on a plaid motion stimulus does not fully transfer to its two components
449 (Figure 5E), we conclude that a significant part of the relevant plasticity occurs
450 downstream from the low-level motion mechanisms. Given the evidence that MT neurons
451 analyze pattern motion by selectively integrating inputs from a population of V1 neurons
452 [38](#), one possible mechanism is that learning improves information transmission from the
453 low-level to the middle-level motion processing. Such a mechanism is consistent with
454 findings of a recent study where attention was shown to improve the amount of
455 information transferred from V1 to hMT+ [50](#). Moreover, learning effects in our study are
456 specific to direction, speed, contrast, and size, indicating critical roles of neuronal tuning
457 to these low-level visual features. For example, stimulus contrast and size have strong
458 influences on neural responses in motion processing [51](#). This is also in line with our
459 previous findings showing that motion perception is strongly modulated by stimulus
460 contrast and size [52,53](#)—behavioral findings that have been linked to mechanisms within
461 area MT [54,55](#).

462 In summary, our study provides evidence for the training-induced plasticity in the
463 intermediate stage of motion processing, and highlights the significance of basic motion-
464 related visual attributes in mediating the transfer of motion VPL.

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