Greater plasticity in lower-level than higher-level visual motion processing in a passive perceptual learning task

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Simple exposure is sufficient to sensitize the human visual system to a particular direction of motion, but the underlying mechanisms of this process are unclear. Here, in a passive perceptual learning task, we found that exposure to task-irrelevant motion improved sensitivity to the local motion directions within the stimulus, which are processed at low levels of the visual system. In contrast, task-irrelevant motion had no effect on sensitivity to the global motion direction, which is processed at higher levels. The improvement persisted for at least several months. These results indicate that when attentional influence is limited, lower-level motion processing is more receptive to long-term modification than higher-level motion processing in the visual cortex.

A central issue in neuroscience is to clarify how the brain selectively adapts to important environmental information[1–5]. A large body of evidence indicates that modification of visual processing is driven by task demands[6–34]. In addition to such task-driven perceptual learning (TDL), the visual system can also adapt to some stimulus features more passively. In a previous study, we found that after numerous presentations, the human visual system becomes more sensitive to task-irrelevant, subthreshold coherent motion in a stimulus[35]. This suggests that the visual system adapts to frequently presented information of sufficient ecological importance, even when the subject does not actively attend to the stimulus. We call this type of learning 'task-irrelevant perceptual learning' (TIL).

Is there a common mechanism that underlies both task-driven and task-irrelevant learning? To address this question, at least two aspects of visual processing must be clarified for TIL: at what stage(s) in visual processing does learning occur, and how long does the learning last?

These questions have been studied for TDL, which seems to involve a broad range of stages in visual processing. TDL shows a high specificity for stimulus features such as motion direction[8,16,34], orientation[6,7,20] and location[7,9,11,20], as well as for eye of presentation[13]. Because receptive fields are smaller and spatiotemporal resolution and specificity tend to be increased at early stages in the visuocortical hierarchy[36], these findings suggest that TDL plasticity occurs in low-level visual cortical areas. Indeed, single-unit recordings in monkeys show that V1—the lowest cortical stage of visual processing—is involved in task-driven perceptual learning[29,31]. (Similar conclusions have been reached in humans with fMRI[33].) However, a role for V1 in learning does not exclude the possibility that higher stages are also involved[13,19,21,24,26,28]. For example, TDL is accomplished by external noise reduction and signal enhancement, which may reflect plasticity at higher levels that weigh visual input for decision making[24]. It has also been suggested that learning proceeds from higher to lower stages[13,19,28]. Thus, if a single mechanism underlies both task-driven and task-irrelevant learning, multiple stages should be involved in both processes. Our previous study[35] of TIL did not address the question of which visual processing stages are involved.

Another important aspect of perceptual learning is the persistence of learning over time. TDL lasts for at least a few weeks[7,8] and, in some cases, for 2–3 years[13] without further practice of the task. Thus, TDL constitutes long-term learning rather than mere short-term sensitization. Whether TIL is short- or long-lived, however, has yet to be determined.

Here we examined both these issues for motion-direction TIL, because these properties are important for identifying the underlying mechanism(s) for this phenomenon. We presented a motion stimulus as a task-irrelevant feature, and found that performance improved only on local motion, which is processed at a very low-level stage of motion processing, and not on global motion, which is processed at a higher-level stage at which local motion signals are spatiotemporally integrated. We also found that local-motion TIL persisted for at least several months. Thus, although our results show that local-motion TIL and TDL are both long-term effects, they are not processed by the same mechanism. The mechanism underlying TIL may reside only at a very low-level processing stage that probably includes V1 and may be subject to modification mainly by bottom-up signals in the absence of strong top-down attentional influence.

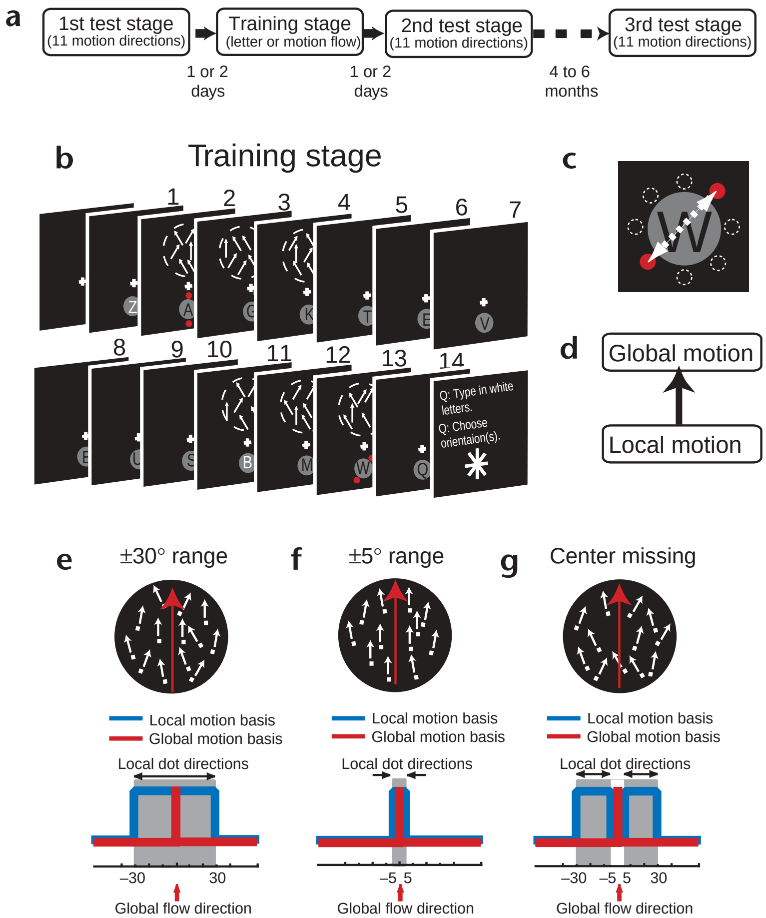

Fig. 1. Methods of the first experiment. (**a**) Overall procedure. (**b**) An example trial in the training stage. A series of letters was presented on a gray circle (1° diameter). A letter appeared 400 ms after the onset of a white fixation cross at the center of a black background. (**c**) A display in which two red disks were presented outside the gray circle. The white arrow with a broken line represents an imaginary interpolated line, showing the orientation the subjects were asked to indicate. The white broken circles represent other possible locations at which a pair of red disks were presented. (**d**) Two stages in early motion processing: local motion is processed before global motion. (**e**–**g**) Top, SCs of the three different ranges within which local dots moved. Local dot motion directions represented as white arrows were evenly distributed within 30° from the mean direction represented as a red arrow (**e**), within 5° (**f**) or within 5–30° on either side of the mean motion direction in the center-missing SC (**g**). Bottom, predicted results for two different possibilities. If learning is based on presented local motion directions, improvement should occur within the range shaded in gray (blue lines). If learning is based on the global motion direction, improvement should occur only at the global motion direction or its vicinity, irrespective of the local motion range (red lines).

Results

In our previous study showing task-irrelevant perceptual learning[35], the task-irrelevant stimulus was a random-dot motion display, in which a small number of signal dots moved coherently (same direction and speed) while the remaining dots moved randomly. As the local direction of the signal dots was the same as the global coherent motion in that display, we could not determine whether improvement occurred for the local or global motion. In the current study, we presented a stochastic cinematogram (SC), in which task-irrelevant local and global motion can be dissociated. In the SC, dots exhibit spatiotemporally local random walks within a particular range of motion directions; observers see individual dots moving locally as well as a global flow. If the number of local directions is evenly distributed, then the global flow appears to move in the direction of the mean of the local motion directions[37–39]. Such global motion flow is processed at a higher stage than local dot motion[37–41] (**Fig. 1d**) as a result of cooperative and/or global interactions among local directional signals[39–44].

What happens when SCs with the same global motion direction and the same range of local motion directions are repeatedly presented as a task-irrelevant stimulus? If TIL occurs at a higher, global-motion level, sensitivity to the global motion direction should be improved, irrespective of the range of local motion directions. In contrast, if the learning occurs at a lower local motion level, sensitivity to the complete range of local directions should be improved, irrespective of the global motion flow direction. And, as receptive field sizes are larger at higher stages[36], if the learning occurs at the higher level, the gain should be spatially more extensive than if it occurs at the lower level.

The first experiment consisted of a training stage and three test stages. During training, SCs with the same global motion direction and the same range of local motion directions were repeatedly presented to a particular subject as a task-irrelevant stimulus while the subject performed two attention-demanding central tasks on stimuli presented in a different location from the SC. To examine the short-term effects of exposure to the SC, we tested the discriminability of 11 motion directions 1–2 days before and after training. The final test was done 4–6 months after the training stage to determine whether TIL is long-term learning or merely short-term sensitization (**Fig. 1a**).

In each trial of the training stage, a sequence of 14 letters (2 white target letters and 12 black non-target letters) was presented below a fixation cross for half the subjects (four subjects for each of the three SCs presented) and above the cross for the other half (**Fig. 1b**). A pair of red dots was also presented twice at randomly determined times just outside the gray circle on which the letters were shown. An SC was presented on the vertically opposite side of the display from the letters and red dots (**Fig. 1b** and **c**). Subjects performed first an RSVP (rapid serial visual presentation) task[35,45–47] and then two orientation tasks. After the disappearance of the letter sequence, red dots and SCs, subjects were instructed to report the two white target letters for the RSVP task and then to indicate the orientation of the imaginary lines passing through each of the two pairs of red dots for the orientation indication task (**Fig. 1b** and **c**). Both the global motion and the local motion perceived in the SC were task-irrelevant features. Simultaneous or nearly simultaneous presentation of the SC and the letters and red dots should

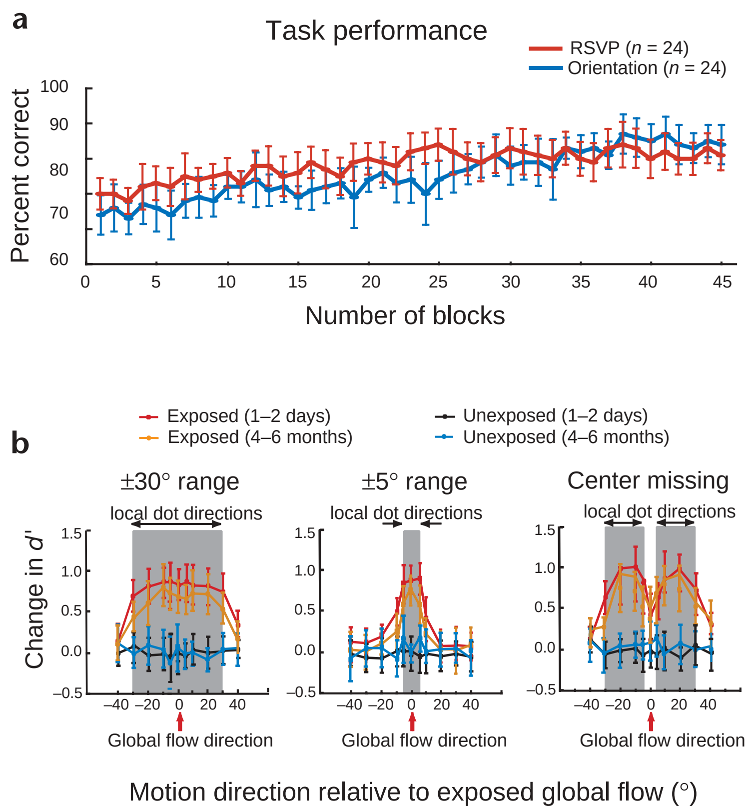

Fig. 2. Results of the first experiment. (**a**) Mean (n = 24) time course performances of the letter identification (RSVP) task (red) and the orientation indication task (blue) in the training stage. Vertical bars represent standard errors across subjects. (**b**) Mean performance improvement (change in d') in the discrimination of 11 coherent motion directions for the ±30° range (left), ±5° range (center) and the center-missing range (right). Performance improvement is defined as d' in the test stage conducted before training, subtracted from that in the second test stage conducted 1–2 days after training (red and black) or subtracted from that in the third stage conducted 4–6 months after training (orange and blue). Positive and negative values represent clockwise and counterclockwise rotations relative to the exposed global motion direction (0°), respectively. Gray zones represent the range of directions within which local dots moved. Common tendencies were found for the three ranges, irrespective of whether improvement occurred at 1–2 days or 4–6 months after training. When tested for the exposed location (red and orange), performance was significantly higher after training for all of the presented local motion directions (within the zones) at 1–2 days or 4–6 months ($P < 0.01$, Wilcoxon signed rank test) and for the directions just outside a range (at 40° for the ±30° range and the center-missing range, for the test at 1–2 days after training, $P < 0.05$). In the unexposed location, performance improvement was not significantly different from zero for any of the tested directions.

greatly reduce attentional resources allocated to the SC (as we confirmed in the third experiment below). The interval between the onset of a white letter and the offset of an SC was ≤ 300 ms, falling within the attentionally taxing interval[45,46] of 500 ms. For each of the three subject groups, the local dots within the SC moved within a different range of directions (in which directions were evenly distributed within the range) of ±30°, ±5° or ±30° with the center ±5° of the range missing. For the ±30° or ±5° ranges, dots moved within 30° or 5° from the mean global flow direction (**Fig. 1e** and **f**, respectively). For the center-missing range, dots moved between 5 and 30° on each side of the mean direction (**Fig. 1g**). For each subject, a global motion direction in the SCs was randomly determined and remained constant throughout training (Methods).

The test stages allowed us to examine how SC exposure in the training stage affected subsequent motion-direction performance. The test stages probed the discriminability of 11 coherent motion directions. The test stimulus was presented either in the same location as the SCs during the training stage (the exposed location) or symmetrically opposite to the exposed location with respect to the center fixation cross (an unexposed location). This allowed us to determine whether the learning benefits that resulted from SC exposure would transfer to another location. In each trial, subjects indicated whether two successively presented test stimuli had matching coherent motion directions by striking one of two keys labeled "same" and "different" (Methods).

We predicted that if learning occurred only for local motion, improvement after the training should be within the range at which the local dots moved (blue curves in **Fig. 1e–g**). In contrast, if learning occurred only for global motion, improvement should be only for global motion direction (red curves), irrespective of the ranges of local motion directions.

All subjects showed a gradual but steady improvement in performance on the RSVP and orientation indication tasks in training (**Fig. 2a**). Results from the three test stages are shown in **Fig. 2b**. For the exposed location (whether training and testing were separated by 1–2 days or 4–6 months), performance improved for all the tested directions within the range of directions in which the local dots moved. Outside those ranges, however, no significant improvement was found for most directions (gray zones in **Fig. 2b**). There was no performance improvement for any of the directions in the unexposed location. Thus, repetitive exposure to local and global motion as irrelevant features resulted in perceptual learning only for the local dot directions and not for the global flow directions. As local motion is processed at a lower stage than global flow motion[37–41], this result indicates that TIL occurred only at the lower stages of motion processing.

To test the possibility that global motion learning might require more presentations than local motion learning, we extended the number of training blocks to 78 with four new subjects and still found no learning for the global motion. In addition, for the exposed location, local-motion learning persisted several months after the offset of the training stage, indicating that the improvement represents long-term learning rather than mere short-term sensitization. Moreover, the local-motion TIL occurred in the exposed location but not in the unexposed location. This indicates that local-motion TIL is location specific. All these results are in accord with the hypothesis that local-motion TIL occurs at the lower, local motion stage rather than at the higher, global motion stage.

Is this local-motion TIL influenced in the presence of a glob-

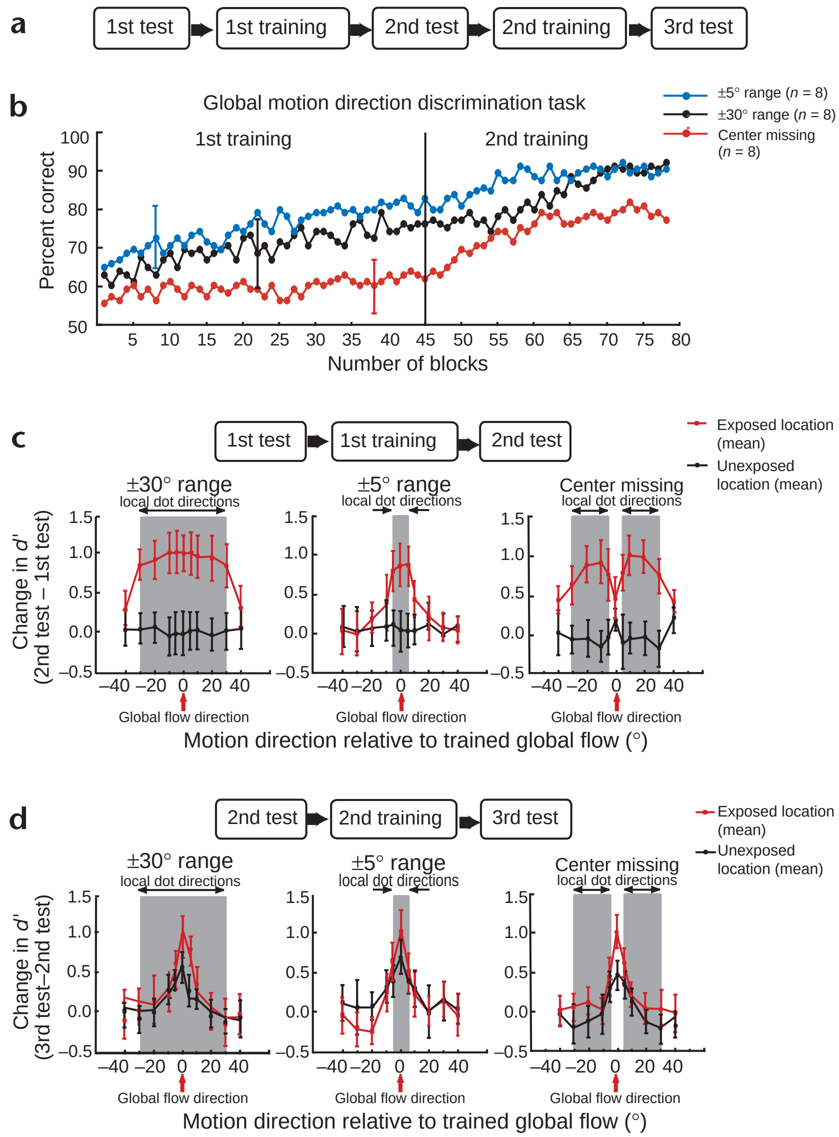

Fig. 3. Procedure and results of the second experiment. (**a**) Overall procedure. (**b**) Percent correct for the global motion discrimination task conducted in the training stages for the three ranges with three different groups of eight subjects. Vertical bars represent the mean standard error between individuals for each range. (**c**) The mean performance change (change in *d*′) for the coherent motion discrimination task from the first to the second test stages. Change is defined as the subtraction of performance (*d*′) in the first test stage (before training) from that in the second test stage (1–2 days after training). The curves for the exposed and unexposed locations are strikingly similar to those in the first experiment. Performance change was significantly greater than zero for all the directions within the range ($P < 0.01$, Wilcoxon signed rank test) and some directions just outside the range ($P < 0.05$ at ±40° for the ±30° range, at ±10° for the ±5° range and at 0° and ±40° for the center-missing range). (**d**) Performance change (in *d*′) from the second to third test stages (the mean and a representative subject), calculated by subtracting performance at 1–2 days after training from performance 4–6 months later. The curves for the exposed and unexposed locations are similar in that the peaks occurred at the trained global motion direction and did not depend on a range of local motion directions. The performance change was significantly greater than zero for –5° to +10° ($P < 0.01$) in the exposed location and –5° to +5° ($P < 0.05$) in the unexposed location for the ±30° range, for –5° to +5° ($P < 0.05$) in the exposed location and –5° to +10° ($P < 0.05$) in the unexposed location for the ±5° range, and for –5° to +10° ($P < 0.05$) in the exposed and unexposed locations for the center-missing range.

al motion direction discrimination task, which should be processed at a higher-level stage? We carried out a second experiment to address this question. A new group of subjects was trained to discriminate global flow directions of SCs. Global motion direction was now a task-relevant feature, while the letters, red dots and local motion were task-irrelevant. The procedure was identical to the first experiment, except that a complete experiment consisted of three test stages and two training stages (**Fig. 3a**), and subjects were instructed to judge whether or not the global motion directions in two SCs matched, while ignoring other presented stimuli, such as letters and red dots (Methods).

All subjects showed gradual improvement during training (**Fig. 3b**). More importantly, the results of the test stages indicate that in the early phase of learning, performance gain occurred for the ranges of directions of local dot motion (**Fig. 3c**). The patterns of learning in all three range conditions (both in shape and magnitude) were strikingly similar to those obtained in the first experiment. Performance (*d*′) improved for all the tested directions within the range and some directions just outside the range. The striking similarity of the curves obtained as a result of the same frequency of presentation of SCs (45 blocks) as in the first experiment suggests that the learning gain for a range of local motion was obtained whether the global motion was task-relevant or task-irrelevant. In a later phase, there was learning gain only for the task-relevant global motion direction; that is, only in response to task demands (**Fig. 3d**). Moreover, whereas early-stage performance gain was seen only for the exposed location (red in **Fig. 3c**), in the later stage it was obtained in both the exposed location and in the unexposed location (red and black in **Fig. 3d**). Thus, in the later phases, the learning benefit spatially extended beyond the exposed region. These results are in accord with the hypothesis that TIL is formed on the basis of the presented local directions, irrespective of whether higher-level global motion is task-relevant or not.

In the first experiment, the presentation of letters and red

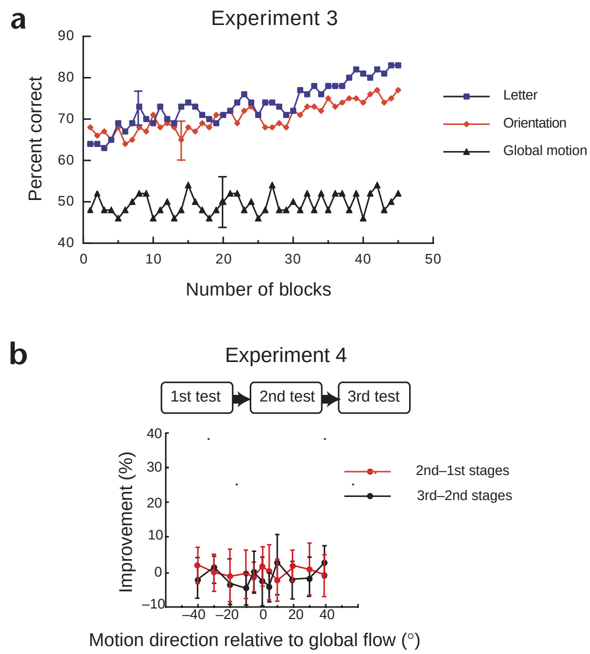

Fig. 4. Results of the third and fourth experiments. (**a**) Third experiment. Percent correct for the letter identification task, the orientation indication task and the global motion direction discrimination task as a function of the number of blocks (days). The mean performances for the three ranges for the global motion discrimination condition were around chance, and so they were averaged. Vertical bars represent the mean standard error between individuals for each task. (**b**) Fourth experiment. Three test stages were conducted without any training to test whether the preceding test stage(s) affected subsequent stage(s). There was no significant difference in performance between the first and second stages or between the second and third stages.

dots as task-relevant features at nearly the same time as an SC may have greatly reduced attentional resource allocated to the SC. (Even the RSVP task alone reduces attentional resources[45–47].) To confirm that attention to the SC was indeed greatly reduced by our two tasks, we conducted a third, control experiment using the same procedure as in the training stage of the first experiment. There were just a few differences: in 90% of the trials, new groups of subjects were asked to perform an RSVP task and two orientation indication tasks as in the first experiment. In the remaining 10% of trials, subjects were asked to perform the global motion discrimination task as in the second experiment. Performance on the letter identification task and the orientation indication task was similar to performance in the first experiment, but performance on the global motion discrimination tasks was only at chance (**Fig. 4a**). These results are consistent with the hypothesis that the RSVP and orientation indication tasks together, if not entirely, greatly consumed attentional resources that could have been allocated to the global motion discrimination task.

In the first two experiments, it is possible that a preceding test stage might have affected subsequent test stages. To address this, we conducted a fourth experiment in which only three test stages were given, with no training. No significant change was found among the first, second and third test stages (**Fig. 4b**).

Discussion

Here we report four main findings. First, exposure to two task-irrelevant features (local and global motion) processed at different levels of motion processing produced performance improvement only on the lower-level feature. Second, such TIL persists for at least 4–6 months. Third, when global motion direction was task-relevant, at an early phase of learning, improvement was seen according to the task-irrelevant local motion directions rather than to the task-relevant global motion direction. In contrast, in a later phase of learning performance, there was improvement for the task-relevant global motion direction. Fourth, the performance gain for task-irrelevant local motion was restricted to the exposed location, whereas TDL for global motion extended beyond the exposed location.

Our results confirm that the discriminability of global motion direction depends on the range of local motion directions[37,48] (**Fig. 3b**). Performance on the global motion discrimination task in the center-missing condition of the training stage was worse than that in the other two ranges. This result raises the possibility that the relatively small improvement in the direction of the global motion in the center-missing condition (**Figs. 2b** and **3c**) is due to the difficulty of precisely perceiving the global motion direction. However, this is not likely for several reasons. First, within the ±30° and ±5° ranges, there was no significant difference among the performance improvements in any direction, including the direction of global motion (**Figs. 2b** and **3c**). Thus no improvement specific for the global motion direction was found in the ±30° and ±5° conditions, in which global motion was perceived more precisely than in the center-missing condition (**Fig. 3b**). Thus, irrespective of the degree of precision for perceiving a global motion direction, the improvement may not have been observed specifically on the global motion direction. Second, a strikingly similar degree of improvement for the global motion direction was found from the second to third stages for all the local motion ranges of the second experiment (**Fig. 3d**). This suggests that improvement specific for the direction of global motion occurred during the second training stage for all the ranges. Thus, although it is true that global motion was perceived less precisely in the center-missing condition, this may not have affected the result that improvement for presented local motion directions preceded improvement for the global motion direction in the second experiment.

Based on these findings, we propose that TDL and TIL of motion are not processed in the same fashion. Task-irrelevant learning of motion may occur only at a very low-level stage and seems to be processed independently of global motion, whether global motion is task-relevant or irrelevant. In contrast, TDL may occur in multiple stages[13,19,21,24,26,28]. What cortical area is involved in TIL of motion? Local motion is mainly processed in V1, whereas global motion and/or interactions between local motion signals are processed in higher areas, including the middle temporal (MT) region in monkeys[42] and MT+ in humans[43,49,50]. The results of the present study show that TIL occurs only for local motion. Thus, putting these lines of evidence together, we suggest that the learning of task-irrelevant motion is located in very low-level cortical areas, including V1.

It is unlikely that the same mechanism underlies TDL and task-irrelevant passive learning of motion. Both TDL and TIL of motion are long-term learning rather than short-term sensitization. TIL of motion occurs at a very low level of visual processing, which probably includes V1, whereas TDL seems to involve multiple stages. We conclude that, when attentional influence is limited, the lowest-level stages of visual processing may be more receptive to modification in response to some stimuli than higher-level stages.

Methods

Subjects. The subjects were 19–31 years old. For each condition of each experiment, a different group of eight subjects was used, except for the third test stage in the first experiment. All subjects had normal or corrected-to-normal vision and were naive to the purpose of the experiments. Informed consent was obtained from all subjects. The experiments were performed in compliance with relevant laws and institutional guidelines.

Experimental design. Subjects sat 125 cm from the viewing screen with their heads in a chin rest, and were instructed to fixate on a small white cross at the center of the screen (1152 × 870 pixel resolution; 21-inch SuperScan Mc 80 display (Hitachi, Minokamo, Japan) controlled by a Macintosh G3). The luminances of the white, black, gray and red parts of the stimuli were 66.0 cd/m^2, <0.5 cd/m^2, 30.0 cd/m^2 and 45.0 cd/m^2, respectively. During a training trial, each letter was presented for 33 ms, followed by a 17-ms blank. The duration of each sequence was 700 ms. The letter center was 2.0° below the fixation cross for half of the subjects and 2.0° above the cross for the other half. The serial order of the presentation of black and white letters was randomized in each trial. Red dots (0.3° in diameter) were presented for 33 ms. Two SCs were presented for 150 ms each in temporally random positions with a blank interval lasting at least 100 ms between them. In an SC, 100 white dots (1 pixel size) moved at 12°/s against a black background within an invisible circular aperture of 5° radius. Each dot moved in one direction for 0.9°, then changed direction for another 0.9°, and so on. The subjects were instructed to press a designated computer keyboard key for each of the two white letters during an RSVP task and to choose among four lines (vertical, horizontal, oblique tilted 45° clockwise or oblique tilted 45° counterclockwise) by moving a cursor and clicking on the line for each of the orientation indication tasks. Each training block consisted of 960 trials that lasted approximately 1.5 h. Each block occurred on a different day, for a total of 45 blocks (the number of blocks by which three subjects had a performance asymptote in a preliminary test). During test stages, the discriminability of 11 directions (–40, –30, –20, –10, –5, 0, 5, 10, 20, 30, and 40° from the trained global flow direction) was measured. Positive and negative values represent clockwise and counterclockwise rotations from the trained global flow direction (0°). The number, size and speed of dots in the test stimuli were the same as those in an SC. In each trial, two test stimuli were presented successively for 150 ms with a 50-ms blank interval. In half the trials, the coherent motion direction of two test stimuli was the same. In the other half, the direction of the second stimulus was rotated by approximately 5° either clockwise or counterclockwise from that of the first RDC. The order of an exposed or unexposed location was varied randomly from trial to trial. No accuracy feedback was given during the training or test stages. Eye movements were monitored for all the subjects in both the training and test stages by a ViewPoint EyeTracker 2.8.2 (Arrington Research Inc., Mesa, Arizona). Trials were excluded when movements beyond the 0.3° resolution of the eye tracking system were detected. Minimal subject attrition (from the eight subjects that served in each of the original conditions) occurred during the third test stage, which was conducted 4–6 months after the end of the training stage (n = 6, 7 and 6 for the ±30°, ±5° and center-missing stages, respectively).

Second experiment. To equate the number of trials with that of the first experiment, the first training stage was terminated when the number of blocks reached 45. The second training stage was terminated at the 78th block, the point at which preliminary data had shown performance asymptotes for all three of the ranges. In half the trials, the global flow direction matched. In the other half, the global direction in the first SC was constant while global direction in the second SC was rotated ±5°.

Third experiment. If a beep sound was presented immediately after the last letter of a sequence disappeared, the subjects were instructed to perform the global motion direction discrimination task instead of the RSVP and orientation discrimination tasks. The beep was presented only on 10% of the trials. In the remaining 90% of trials, no beep was presented, and the subjects were instructed to perform the RSVP task and the orientation discrimination tasks.

Fourth experiment. There was no training stage in the fourth experiment. However, the time intervals (days) between test stages were equated with the averaged intervals in the second experiment.

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Competing interests statement

The authors declare that they have no competing financial interests.

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