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Task-irrelevant perceptual learning specific to the contrast polarity of motion stimuli

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ABSTRACT

Studies of perceptual learning have focused on aspects of learning that are related to early stages of sensory processing. However, conclusions that perceptual learning results in low-level sensory plasticity are of great controversy, largely because such learning can often be attributed to plasticity in later stages of sensory processing or in the decision processes. To address this controversy, we developed a novel random dot motion (RDM) stimulus to target motion cells selective to contrast polarity, by ensuring the motion direction information arises only from signal dot onsets and not their offsets, and used these stimuli in conjunction with the paradigm of task-irrelevant perceptual learning (TIPL). In TIPL, learning is achieved in response to a stimulus by subliminally pairing that stimulus with the targets of an unrelated training task. In this manner, we are able to probe learning for an aspect of motion processing thought to be a function of directional V1 simple cells with a learning procedure that dissociates the learned stimulus from the decision processes relevant to the training task. Our results show learning for the exposed contrast polarity and that this learning does not transfer to the unexposed contrast polarity. These results suggest that TIPL for motion stimuli may occur at the stage of directional V1 simple cells.
1. Introduction

The question regarding the stages of brain processing at which perpetual learning takes place is a topic of great controversy. While some studies have argued that perceptual learning can take place at early stages of sensory processing (Furmanski, Schluppeck, & Engel, 2004; Schoups et al., 2001; Watanabe et al., 2002), other studies have made the case that most of the learning takes place at late stages of sensory processing or at decision stages (Dosher & Lu, 1998; Law & Gold, 2008; Smirnakis et al., 2005; Xiao et al., 2008). A likely resolution of this long-standing controversy is that the degree to which learning occurs at lower- or higher-level processing stages may depend on task difficulty/precision (Ahissar & Hochstein, 1997; Jeter et al., 2009) and training procedure (Xiao et al., 2008). An interesting paradigm that may lead to a greater degree of low-level sensory plasticity is that of task-irrelevant perceptual learning (TIPL).

Studies of TIPL have made the remarkable discovery that the brain can refine its sensitivity to stimulus features in the environment even when they are presented without awareness or focused attention (Watanabe, Sasaki, & Nanez, 2001). This paradigm is relevant because in the absence of attention, human lateral prefrontal cortex, which is known to subserve high-level functions such as cognitive control and decision-making, has been shown to be less active in response to subliminal and parathreshold motion stimuli in comparison to suprathreshold stimuli (Tsushima, Sasaki, & Watanabe, 2006). Also, TIPL has been shown to occur only for parathreshold stimuli (Tsushima, Seitz, & Watanabe, 2008). In other words, plasticity in the decision processes seems an unlikely account for TIPL. Also, TIPL dissociates what is being learned (i.e., the task-irrelevant stimulus) from the decision processes that correspond to the training task.

While studies using the paradigm of TIPL have generated much attention, they have to date mostly focused on when learning occurs and have revealed that for TIPL to occur, the task-irrelevant stimuli should be perceptually neither too weak nor too strong (Tsushima et al., 2008), as mentioned above, and either attention needs to be engaged on task-relevant stimuli (Seitz et al., 2005) or external rewards need to be delivered (Seitz, Kim, & Watanabe, 2009) so that reinforcement learning signals can spill over to spatiotemporally nearby task-irrelevant stimuli (Nishina et al., 2007; Seitz & Watanabe, 2003). In this present study, however, we are interested in questions regarding what can be learned and where in the brain does plasticity occur during TIPL.

Notably Watanabe et al. (2002) suggested that in regard to motion stimuli, TIPL occurs at a low-level of motion processing because learning was found only for the local motion directions but not the global direction of a task-irrelevant dynamic dot display. However, the type of motion processing cells that provide the substrate for this directional learning is still unknown as local directional cells include directional V1 simple and complex cells, and possibly MT neurons (Majaj, Carandini, & Movshon, 2007). Thus it is unclear whether the learning observed by Watanabe et al. (2002) resulted from a later stage of motion processing, such as in MT or the readout from MT to LIP (Law & Gold, 2008), or whether it occurred at an earlier stage of processing, such as in directional V1 cells. In the present study, we attempt to disambiguate the roles of these potential sites in TIPL by testing whether TIPL is specific to the contrast polarity of the task-irrelevant motion stimulus. Coding of local motion specific to a contrast polarity is thought to occur at a short-range motion filtering stage of directional V1 simple cells, before pooling of signals between contrast polarity occurs as part of a long-range motion filtering stage at MT or beyond, as predicted by the 3D Formotion model (Berzhanskaya, Grossberg, & Mingolla, 2007; Chey, Grossberg, & Mingolla, 1997; Grossberg, Mingolla, & Viswanathan,
Thus, if learning is found to not transfer to the opposite contrast polarity, then it is suggestive that TIPL for motion may take place at an early stage of motion processing in V1.

Figure 1.

2. Experiment
In the primate motion processing pathway, neuronal selectivity to motion direction first appears in V1. Physiological and psychophysical studies have together provided strong evidence for the segregation of early motion processing cells into the ON and OFF channels (see Figure 1). Directional V1 simple cells are sensitive to the contrast polarity of the motion stimuli; however, by the stage of stage of directional V1 complex cells, the ON and OFF channels are combined, and these cells and those at later stages of motion processing have responses that are invariant to the contrast polarity of motion stimuli (Goodwin & Henry, 1975; Movshon & Newsome, 1996). Thus evidence that TIPL is specific to the contrast polarity of motion stimuli would be consistent with learning that may occur at the stage of directional V1 simple cells, and evidence that TIPL transfers between contrast polarities would be consistent with learning occurring at a later stage of motion processing.

Figure 2.

To test this we designed a polarity-specific RDM stimulus based upon a technique by Wehrhahn and Rapf (2001) that was devised to selectively activate ON or OFF cells by ensuring that the two spatially offset flashes that constitute an apparent motion stimulus have different onset but simultaneous offset times (see Figure 2a). Using this extended approach, we were able to create polarity-specific multi-frame RDM stimuli of variable coherence. Depending on whether the stimulus is of the ON or OFF type, the dots are shown at a luminance level of either 108 cd/m² or ~0 cd/m² on a gray background (54 cd/m²). In our RDM algorithm, whenever a dot from a given frame is chosen to move in the signal direction, it persists at its current location in the next frame too. And this persistence lasts until the dot is chosen to become noise, i.e., relocated to a random position (see Figure 2b). Given that high coherences promote longer signal dot lifetimes, the above modification may create strong motion tails, which can encourage signal dot tracking and confound bottom-up processes involved in direction discrimination. To reduce this effect, the lifetime of signal dots is limited to two frames whenever possible. For coherences used in our study (<= 50%), this can always be ensured.

Figure 3.

Figure 4.

The basic procedure, based on Seitz and Watanabe (2003), was as follows. We first assigned each of our human subjects (n = 7) to a designated contrast polarity and motion direction (from one of four non-cardinal directions; 22.5°, 112.5°, 202.5° and 292.5°). The experiment comprised five exposure sessions and two testing sessions, one before and the other after the exposure stage. The testing sessions measured the subjects’ ability to discriminate the direction of random dot motion stimuli shown for 400 ms in various coherence (3%, 5%, 10%, 15%, and 25%), signal direction and contrast polarity conditions, allowing the assessment of
TIPL (see Figure 3). In each exposure session, subjects were repetitively exposed to their designated contrast polarity-specific RDM stimuli at 10% coherence in the periphery while they were required to solely perform an attentionally demanding RSVP task in the fovea. The targets in each RSVP task trial were temporally paired with dots moving in the designated direction; the distracters co-occurred with those in other directions (see Figure 4). The detailed description of the experimental methods is provided in Section 3 below.

3. Methods

3.1. Subjects
A total of n = 7 human subjects (18-30 years; four female, three male) were recruited from amongst students of Boston University. They were naïve to the purpose of the experiment and gave written informed consent to their participation for which they received compensation. The methods of the study were approved by the Institutional Review Board of Boston University Charles River Campus.

3.2. Apparatus
All stimuli were viewed binocularly at a distance of 60 cm on a 36 cm horizontally wide Dell M992 monitor that was set to a resolution of 1024 x 768 and a refresh rate of 85 Hz. A chin-rest was used to stabilize the head, and the monitor center was ensured to be approximately in the same horizontal plane as that of the subjects’ eyes. The experiment was controlled using Psychtoolbox Version 2 (Brainard, 1997; Pelli, 1997) from MATLAB 5.2.1 (The MathWorks, Inc.) on a Macintosh G4 machine running OS 9.

3.3. Rapid serial visual presentation (RSVP) task
The RSVP task required subjects to focus on a temporally changing sequence of characters consisting of two numbers and six alphabets in random order and to report the two numbers (or targets) at the end of each trial. The two numbers/targets were randomly chosen without replacement from the set: (‘1’, ‘2’, ‘3’, ‘4’) and the six alphabets/distracters from the set: (‘A’, ‘E’, ‘F’, ‘H’, ‘K’, ‘M’, ‘N’, ‘P’, ‘V’, ‘W’, ‘X’, ‘Y’). The possible alphabets had been screened for confusability with any digit (0-9). Each character at the screen center subtended an angle of ~0.8°.

In a typical trial, the eight characters were shown successively in the center of the screen with each character displayed for 275 ms and followed by a blank period of 125 ms. Then following a delay period of 500 ms during which a green 0.2° fixation point appeared in the center, the subject had 4000 ms within which to press the two numbers, observed during the sequence presentation, on a keyboard. The trial was considered to be correct only if the two numbers were entered in the order in which they appeared. The next trial began after an interval of 400 ms.

3.4. Direction discrimination task
In the direction discrimination task, subjects on each trial were asked to choose which of four alternative arrows matched the coherent direction of an RDM stimulus. In each trial, random dot motion (RDM) in some signal direction at some coherence level and specific to a contrast polarity (either ON or OFF) was shown at 12°/s speed in an invisible 12° diameter aperture centered on the screen. Each dot at the screen center subtended an angle of ~0.1°. Dot density was fixed at 16.7 dots deg⁻² s⁻¹. ON (OFF) dots were shown at a luminance level of 108 cd/m²
(-0 cd/m²) on a gray background (54 cd/m²). Given the dot speed and monitor refresh rate values, the spatial and temporal displacements between consecutive signal dot flashes in the stimuli were 0.14° and 11.76 ms, which are both below the classical D_max (0.25°) and T_max (100 ms) values from Braddick’s initial studies (Braddick, 1974) for the directional short-range process; however, note that several later studies have shown how these spatial and temporal limits are fluid given different stimulus parameters.

In a typical trial, the dots were shown around a 0.2° green fixation point for 400 ms followed by a delay period of 500 ms. Then the directional response was recorded by clicking within 4000 ms near the appropriate one of four directional bars, which appeared on the screen projecting from the fixation point. The next trial began after an interval of 400 ms. In order to minimize top-down contributions to performance, subjects were specifically instructed to not engage in individual dot tracking, and instead make the directional decision while fixating the point in the screen center.

3.5. Procedure
The procedure was based on that used in Seitz and Watanabe (2003). The experiment comprised eight one-hour sessions, each on a different day. The first session was a practice session that was used to familiarize subjects with the tasks and stimuli and to determine thresholds of performance. The second and eighth sessions used the direction discrimination task to measure performance on the motion stimuli. The third-to-seventh sessions were training sessions employing the RSVP task. The session days were as consecutive as they could be scheduled. All sessions were conducted in a dark room.

3.5.1. Practice session (Day 1)
The first session was primarily for the subjects to get acclimatized to the experimental conditions. It comprised of two practice tasks: an RSVP task and a direction discrimination task.

In the practice RSVP task, the luminance of the characters was randomly varied from trial to trial. Five luminance levels with respect to the gray background (54 cd/m²), ranging from 47.4 cd/m² to 52.4 cd/m², were tested at 10 trials per level. A side goal of this task was to roughly determine the luminance level at which the initial performance is neither too low nor too high (~75%). Based on the obtained data, 51 cd/m² was chosen as the luminance level for the RSVP task characters during the exposure sessions.

In the practice direction discrimination task, the RDM stimulus direction and coherence were randomly varied from trial to trial within two randomly ordered blocks corresponding to the two polarities. Four non-cardinal directions (22.5°, 112.5°, 202.5°, and 292.5°), five coherence levels (5%, 10%, 15%, 25%, 50%) and the two contrast polarities were used at five trials per condition. Only in this practice task, visual and auditory feedback was given for each trial as to whether the response was right or wrong. A side goal of this task was to roughly determine the coherence level from the resulting psychometric functions where the overall performance was neither too weak nor too strong. Based on the obtained data, 10% coherence level was fixed for the task-irrelevant motion stimuli employed during the exposure sessions. This value is within the range for which TIPL has been found in other experiments (Tsushima et al., 2008).

3.5.2. Pre-exposure testing session (Day 2)
The goal of this session was to measure the baseline discrimination performances in response to RDM stimuli corresponding to the four directions and the two contrast polarities, so that the effect of exposure (in the absence of attention) could be assessed later.
It involved the direction discrimination task, similar to the one in the practice session. The four directions (22.5°, 112.5°, 202.5°, and 292.5°), five coherence levels (3%, 5%, 10%, 15%, 25%) and the two contrast polarities were tested at 30 trials per condition. No response feedback was given. The 1200 trials were arranged into 20 blocks. Half of the blocks were randomly assigned to one contrast polarity and the other to the opposite polarity. Within each block, conditions corresponding to various directions and coherences were randomly interleaved. The idea behind the piecewise block design was to reduce any non-stationarities in motion processing that may occur due to arbitrary changes in contrast polarity of the motion signals from trial to trial. Subjects had an opportunity to take a short rest after the completion of every 5 blocks.

3.5.3. Exposure sessions (Days 3-7)
Of 7 subjects, 3 were randomly selected to be exposed to ON random dot motion stimuli and the other 4 to OFF stimuli. Also, each subject was randomly assigned a (designated) direction.

The goal of these sessions was to repeatedly expose the subjects to parathreshold (10% coherence) motion stimuli while their attention is focused elsewhere, on the RSVP task. Each exposure session comprised 440 RSVP task trials. Unlike in the practice session, the RSVP characters (51 cd/m²) in each trial co-occurred temporally with designated contrast polarity-specific motion stimuli (either ~0 or 108 cd/m²), each of which was presented for 400 ms around the character, on the gray background (54 cd/m²). The target numbers co-occurred with motion stimuli in the designated direction, and the distracters co-occurred with motion stimuli in other directions on an equal random basis. The temporal midpoints of the durations for which an RSVP character and its corresponding motion stimulus were presented, respectively, coincided. The two numbers appeared one each in the two halves of the sequence in order to avoid trials in which both numbers are presented early on, causing subsequent leakage of attention to the motion stimuli. Subjects were specifically instructed to ignore the motion stimuli surrounding the RSVP characters as they were irrelevant to the RSVP task at hand. Subjects had an opportunity to take a short rest after the completion of every 110 trials.

3.5.4. Post-exposure testing session (Day 8)
The post-exposure testing session was identical to the pre-exposure testing session. The goal here was to measure learning that may have occurred due to the motion stimuli of designated direction and polarity that were exposed during the RSVP task.

3.6. Data analysis
A 2-way repeated measures ANOVA was conducted with Direction x Polarity as factors. Right-tailed paired t-tests were conducted on various relations between changes in performance found in conditions of interest.

Figure 5.

4. Results
As one would expect, the RSVP task performance gradually increased through the five training sessions (see Figure 5). These data show that subjects were generally engaged in the RSVP task during the exposure phase of the study and that they were undergoing task-relevant learning.

Figure 6.
In regard to learning for the task-irrelevant motion stimuli, we found that TIPL was specific to the exposed contrast polarity (see Figure 6), which reflected in a significant effect of polarity \( p = 0.021 < 0.05 \), repeated measures ANOVA. For the paired direction, the average improvement in performance was significantly greater under the exposed polarity in comparison to the unexposed polarity \( p < 0.05 \), right-tailed paired t-test) and while highly significant learning was observed under the exposed polarity \( p < 0.001 \), right-tailed paired t-test), there was no significant learning under the unexposed polarity \( p = 0.2 \), right-tailed paired t-test). Significant learning for the paired direction under exposed polarity, but not unexposed polarity was observed for either polarity considered separately (right-tailed paired t-tests: \( p < 0.05 \) for each of the ON and OFF exposed polarities; \( p = 0.19 \) for unexposed ON polarity; \( p = 0.35 \) for unexposed OFF polarity). For the exposed polarity, more learning occurred for the paired direction than for the control, unpaired, directions \( p < 0.05 \), right-tailed paired t-test), but there was no difference in learning neither between the paired and control directions under the unexposed polarity nor between the two polarity conditions for the control directions. But for the control directions, there was significant learning under both contrast polarity conditions. This learning can possibly be explained by baseline shifts, i.e., consolidation of learning after the pre-exposure testing session and online learning during the post-exposure testing session. Detailed statistical test results are provided in Table 1. In sum, we found that TIPL was specific both to the direction and the contrast polarity of the motion stimuli that were paired with the targets of the RSVP task.

Table 1.

5. Discussion
Our results confirm that task-irrelevant perceptual learning is specific to the contrast polarity of the exposed motion stimuli. These results are difficult to explain by changes in either later stages of sensory processing because motion processing beyond directional V1 simple cells is contrast polarity-invariant or decision stages because the decisions for the training task were dissociated from the decisions required during testing. Thus the results suggest the intriguing conclusion that plasticity for TIPL may occur in directional V1 simple cells.

These data support the prediction of the 3D Formotion model that short-range directional filters generate V1 cells sensitive to motion direction and contrast polarity, before projecting to area MT or beyond via long-range directional filters that pool between opposite contrast polarities and begin the process of global motion summation and capture (Berzhanskaya et al., 2007; Chey et al., 1997; Grossberg et al., 2001), which was not found to adapt during TIPL (Watanabe et al., 2002).

Our general conclusion is consistent with previous TIPL studies that showed task-irrelevant learning specific to retinal location (Watanabe et al., 2002) and the eye of exposure (Seitz et al., 2009). The question of whether perceptual learning in the presence of attention may also have an early cortical basis is beyond the scope of the current work. Notably, previous research using different methods found task-relevant learning to transfer between contrast polarities (Wehrhahn & Rapf, 2001). Also, while a previous study (Grieco, Casco, & Roncato, 2006) showed texture learning specific to contrast polarity, their learning procedure does not preclude the attribution of underlying neural plasticity to the readout from V1 simple cells to decision stages. In all, our results suggest that TIPL may differ from task-relevant learning in its
degree of featural specificity and that TIPL can lead to greater proportion of plasticity to arise at early stages of sensory processing.
References


Table 1. Detailed statistical test results. The legend used in the first column is as follows: \(d\): paired direction; \(D\): control directions; \(e\): exposed polarity; \(u\): unexposed polarity. Each entry in the second column specifies the p-value of the right-tailed paired t-test performed on the corresponding relation in the first column. The highlighted rows signify the relations that show statistical significance (at least p < 0.05).
Figure 1. Cartoon of how early motion processing is segregated into ON- and OFF-channels, until they summate at the stage of directional V1 complex cells. Several physiological (Alonso, Usrey, & Reid, 2001; Conway & Livingstone, 2003; Goodwin & Henry, 1975; Livingstone, 1998; Movshon & Newsome, 1996; Reid & Alonso, 1995; Schiller, 1982, 1992) and psychophysical (Croner & Albright, 1997; Edwards & Badcock, 1994; van der Smagt & van de Grind, 1999; Wehrhahn & Rapf, 1992) studies support this segregation in the form and motion pathways.
Figure 2. Contrast polarity-specific motion stimuli. (A) A typical apparent motion stimulus, which comprises two brief flashes that occur in different spatial locations at different times, activates both ON- and OFF-cells in early motion processing. However, if the two spatially separate flashes are designed to have the same offset times, then motion cells specific to a single contrast polarity are selectively activated (Wehrhahn & Rapf, 1992). (B) An illustration of a multi-frame variable coherence RDM stimulus that targets OFF motion cells. Here four dots, whose luminance is lower than that of the background, are displayed in each frame with the signal direction being rightward (indicated by white arrow) at 50% coherence, and sample trajectories of the dots are shown for four frames. The number on the dot signifies the frame in which it appears. Temporal luminance profiles are shown at few signal dot locations to illustrate how our modification for RDM stimuli works. Signal dot lifetime is limited to two frames whenever possible to prevent confounding motion tails in response to high coherences.
Figure 3. Schematic of a testing session trial. In this example, a positive polarity-specific RDM stimulus at some coherence in some direction is shown for 400 ms. Following a delay period of 500 ms, the perceived direction can be chosen within 4000 ms from four alternatives that are displayed on the screen. Note that the aperture boundary and arrows in the figure are only for illustrative purposes and are not actually shown.
Figure 4. Schematic of an exposure session trial. Subjects are instructed to focus on a serially presented sequence of characters that consists of six alphabets and two numbers in random order. Their goal is to identify the two numbers, while ignoring the task-irrelevant polarity-specific (OFF in this case) RDM stimuli in the periphery. For each subject, the two number presentations coincide with dots that have net motion in a given direction (22.5° in this case); the six alphabets were randomly paired with other directions equally. RDM stimuli were shown for 400 ms each without an interstimulus interval, and RSVP characters were shown for 275 ms each with an intercharacter interval of 125 ms. A delay period of 500 ms succeeds the sequential presentation of these stimuli, after which the subject can enter the two numbers within 4000 ms in the order in which they were observed during the trial. Note that the aperture boundary and arrows in the figure are only for illustrative purposes and are not actually shown.
Figure 5. RSVP task performance gradually increased through the five exposure sessions. Error bars represent standard error of mean.
Figure 6. Contrast polarity-specificity of task-irrelevant learning? Results show that TIPL is specific to the exposed contrast polarity. Significantly more learning was found in response to paired direction stimuli for the exposed polarity (blue) when compared to the other polarity (red). Data are averaged across coherences, and for the control directions are further averaged across the three unpaired directions. Error bars represent standard error of mean. See Table 1 for detailed statistical test results.