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Visual experience can substantially alter critical flicker fusion thresholds

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Studies of psychopharmacology often use the test of the critical flicker fusion (CFF) threshold as a measure of total information processing. It is true that studies of practice effects have shown that CFF thresholds are remarkably stable within and across multiple days of testing. This study confirms that subjects who undergo CFF testing on sequential days have stable thresholds, but also demonstrates that in subjects who conducted 1 h of motion training per day for 9 days the CFF thresholds increased by an average of 30%. The results show that the perceptual experience of subjects can dramatically alter the CFF thresholds and should be an important consideration in the control of studies employing the CFF as a measure.

KEY WORDS — critical flicker fusion; perceptual learning; perceptual experience; human psychophysics

INTRODUCTION

Critical flicker fusion (CFF) is the lowest level of continuous flicker that is perceived as a steady source of light. Although retinal neurons respond to flicker at rates as high as 120 Hz, perceptual studies show that flicker cannot be detected at frequencies nearly this high. The ability to resolve flicker is thought to be limited by the early visual system (Eysel and Burandt, 1984; Wells *et al.*, 2001).

The CFF has become an important measure in studies of psychopharmacology. It has been shown to be a measure of 'total processing capacity' and has been validated in a number of studies (Hindmarch, 1982; Parrott, 1982). Importantly, multiple methods of evaluating CFF thresholds have been shown to be stable to repeated testing (McClelland, 1987; Parkin *et al.*, 1997).

Plasticity in sensory systems has traditionally been thought to occur only during early development and then to be hard-wired in adults (Marr, 1982). This view has been substantiated by studies of critical period development in which gross plasticity of early visual areas only occurs for a brief period after birth (Hubel and Wiesel, 1965). A challenge to this view has been made by psychophysical studies of perceptual learning (Fiorentini and Berardi, 1980; Poggio *et al.*, 1992; Ahissar and Hochstein, 1997; Chun, 2000; Schoups *et al.*, 2001; Adini *et al.*, 2002), which show that even in adults, perceptual abilities can be sharpened with repeated exposure or training. For example, detection or discrimination thresholds can be reduced and usually show a high degree of specificity with respect to the orientation (Fiorentini and Berardi, 1980; Fahle *et al.*, 1995; Schoups *et al.*, 1995), direction (Ball and Sekuler, 1981; Watanabe *et al.*, 2001; Watanabe *et al.*, 2002; Seitz and Watanabe, 2003), retinotopic location (Fiorentini and Berardi, 1980; Fahle *et al.*, 1995; Dill and Fahle, 1997) and ocularity (Fahle *et al.*, 1995) of the trained visual stimuli. These results are consistent with plasticity of early sensory areas and are supported by neurophysiological evidence of neuronal plasticity in the early visual cortex (Zohary *et al.*, 1994; Gilbert *et al.*, 2001; Schoups *et al.*, 2001; Li *et al.*, 2004; Yang and Maunsell, 2004).

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While studies of perceptual learning have demonstrated plasticity in a large number of visual abilities, it has yet to be tested if CFF thresholds can be modified through training. It was thus decided to test CFF thresholds while training subjects with a learning paradigm that has been shown to improve motion-processing abilities (Watanabe *et al.*, 2001; Watanabe *et al.*, 2002; Seitz and Watanabe, 2003). In this paradigm, subjects are presented with subliminal motion stimuli while conducting an unrelated letter task (Figure 1d). As a result of repeated days of training, subjects develop improved performance of the particular direction of motion presented with the targets of the letter task, perhaps as a result of learning mechanisms similar to conditioning (for details please see Seitz and Watanabe, 2003), Here it is shown that subjects who undergo this training paradigm have significantly improved CFF thresholds.

MATERIAL AND METHODS

Participants

Fourteen participants (age 19–35 years) were recruited from the Phoenix metropolitan area. The subjects were paid the sum of $100 each for participating in the study, and they were required to attend a 1–1.5 h session for 15 of 21 days (no testing occurred during the weekends). The 15 research days consisted of a 3-day pre-test phase in which a total of seven tests were administered, followed by a 9-day exposure stage, and ultimately, a 3-day post-test phase in which the initial seven tests were re-administered (data from a subset of tests are reported here).

All subjects reported good ocular health and had a best-corrected visual acuity (tested on-site) of 20/40 or better (Snellen). Additionally, all participants were naive as to the purpose of the study. Informed consent was obtained from all participants, and this study conformed to the tenants of the Declaration of Helsinki.

Perceptual learning

The perceptual learning paradigm, as described by Seitz and Watanabe (2003), was used for this study. The experiment consisted of three phases (Figure 1). First, in a pre-test, each subject's performance on low luminance contrast and low motion coherence displays was evaluated. Next, in the training phase, subjects completed nine sessions of the letter-pairing task. Finally, in the post-test, each subject's performance was re-evaluated with identical tests as used in the pre-test phase.

For testing sessions, the subject's performance on four directions (70°, 160°, 250°, 340°) of motion was evaluated. For each trial, in all tests, a fixation point appeared for 300 ms, and then a motion stimulus was presented for 500 ms. Subjects were then cued with a response screen to report their answer. The order of tests within each testing phase was randomized across subjects.

In the coherence (Figure 1a) test, subjects were presented with 10% coherence motion, at a contrast of 52 cd/m^2, and asked to choose, with a mouse-click, one of four arrows that corresponds to the direction of the motion stimulus. Each direction was presented 30 times and thus subjects completed 240 trials for each session.

In the contrast test (Figure 1b), subjects were presented with 100% coherence motion at ten, randomly interleaved, contrasts (0, 0.14, 0.2, 0.28, 0.42, 0.6, 0.9, 1, 1.9, 11.8 cd/m^2) and asked to choose, with a mouse-click, one of four arrows that corresponds to the direction of the motion stimulus. Each direction at each contrast level was presented 20 times and thus subjects completed 1600 trials for each session.

In the detection test (Figure 1c), subjects were presented with 100% coherence motion at ten, randomly interleaved, contrasts (0, 0.14, 0.2, 0.28, 0.42, 0.6, 0.9, 1, 1.9, 11.8 cd/m^2) and asked to report, with a key-press, the presence or absence of the motion stimulus. Each contrast level was presented 30 times and thus subjects completed 300 trials for each session.

During each of the 9 days of the exposure stage, subjects conducted a rapid serial visual presentation (RSVP) letter-identification task (Figure 1d). A sequence of eight letters was presented in a central (1°) circle, after which the subject reported the two target letters. The target letters were either light letters in a series of dark distractors, or dark letters in a series of light distractors. Letter presentation was 375 ms temporally centred in a 500 ms motion presentation. Light letters were (5% contrast) and dark letters were (−5% contrast). While the subject did this, 100% coherent motion stimuli in a peripheral annulus (1°–10°) were presented. One motion direction temporally overlapped each target letter (paired direction), and other directions temporally overlapped the distractors (non-paired directions). The paired direction was randomly chosen, from the testing set, for each subject. Motion during the letter task was presented at 100% coherence, but at 0.14 cd/m^2 contrast, with each direction presented for 500 ms. At this contrast level subjects had shown chance performance in the contrast test and reported motion on less than 10% of trials on the detection task.

CFF thresholds

A macular pigment densitometer (Wooten *et al.*, 1999) was used as the measuring device for critical flicker fusion (CFF) threshold. The CFF thresholds were calculated psychophysically by measuring a subject's sensitivities to lights at wavelengths ranging between 460 nm and 550 nm, using the method of heterochromatic flicker photometry. As an internal control, the test subjects were divided into two experimental groups: the 'across-time' group and the 'pre-test, post-test' group. The four subjects in the across-time group had their CFF threshold measured every day during the pre-tests and post-tests, as well as every day during the 9-day exposure stage. Meanwhile, the three members of the pre-test, post-test group had their CFF threshold measured only during the 6 days of the pre-tests and post-tests. Additionally, two control groups of three members each were recruited to have their CFF thresholds measured in a fashion similar to that of the experimental groups (i.e. across-time and pre-test, post-test), but these subjects did not conduct the perceptual learning sessions.

All stimuli were presented in Maxwellian view, and participants used a chin rest throughout this part of the study. Critical flicker fusion was presented as a uniform spot consisting of 1° of visual angle focused in a circular region surrounding the fovea. For purposes of heterochromatic flicker photometry, green (peak wavelength = 550 nm) and blue (peak wavelength = 460 nm) light-emitting diodes were used. Chromatic flicker was measured through equal counter-phased modulations of the green light source, with the blue light modulations being fixed. The experimenter adjusted the rate of green modulation, and the participant was unable to see either the control box or the researcher's actions. Critical flicker fusion threshold was defined as the mean difference between the Hz at which the participant could no longer detect flicker in the stimulus and the Hz at which the participant reported the flicker recommenced.

Statistics

A Bonferroni correction was used to control for multiple comparisons. With five *t*-tests and two ANOVAs the significance of rate $p < 0.05$ was corrected to $p < 0.007$. For tests of learning of each direction in the coherence tests, the performance difference was compared between the pre-test and post-test to a null learning rate of 0 using two-tailed *t*-tests. For the contrast psychometric curve a two-way ANOVA was used to compare performance between the pre-test and post-test.

RESULTS

The perceptual learning paradigm, as described by Seitz and Watanabe (2003), was used for this study. The experiment consisted of three phases (Figure 1). First, in a pre-test, each subject's performance on low luminance contrast and low motion coherence displays was evaluated. Next, in the training phase, subjects completed nine sessions of the letter-pairing task. Finally, in the post-test, each subject's performance was re-evaluated with identical tests as used in the pre-test phase. Eight subjects completed the perceptual learning sessions and six subjects completed the CFF control conditions.

The tests of motion sensitivity showed an improvement for the trained direction of motion (Figure 2). In Figure 2a,b psychometric contrast curves are shown for the paired-direction (that shown with the letter targets) and the non-paired directions before and after learning. Subjects showed significantly improved performance for the paired direction (Figure 2a) after learning ($p < 0.001$, ANOVA), but not for the non-paired directions ($p = 0.31$, ANOVA; see Figure 2b). Additionally, the ability of subjects to detect the paired direction in low motion coherence displays improved significantly ($p < 0.001$, *t*-test), but there was no significant change for the non-paired directions of movement (Figure 2c).

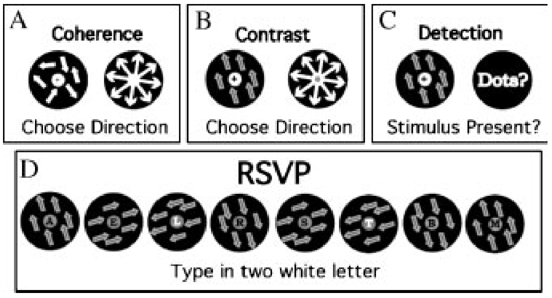

Figure 1. Schematic of experimental procedure. A,B in coherence (A) and contrast (B) tests, subjects were presented with motion stimuli and reported the direction of each stimulus. C, in the detection test, subjects were presented with identical stimuli as in the contrast test, but reported whether or not they saw the motion stimulus. D, in letter-pairing training eight foveally presented letters were displayed and the subject reported the two target letters after the sequence. One motion direction temporally overlapped each target letter (paired direction), and other directions temporally overlapped the distractors (non-paired directions). The motion display was chosen to be at a luminance below the subject's perceptual threshold, as evaluated by the detection and contrasts tests (see methods)

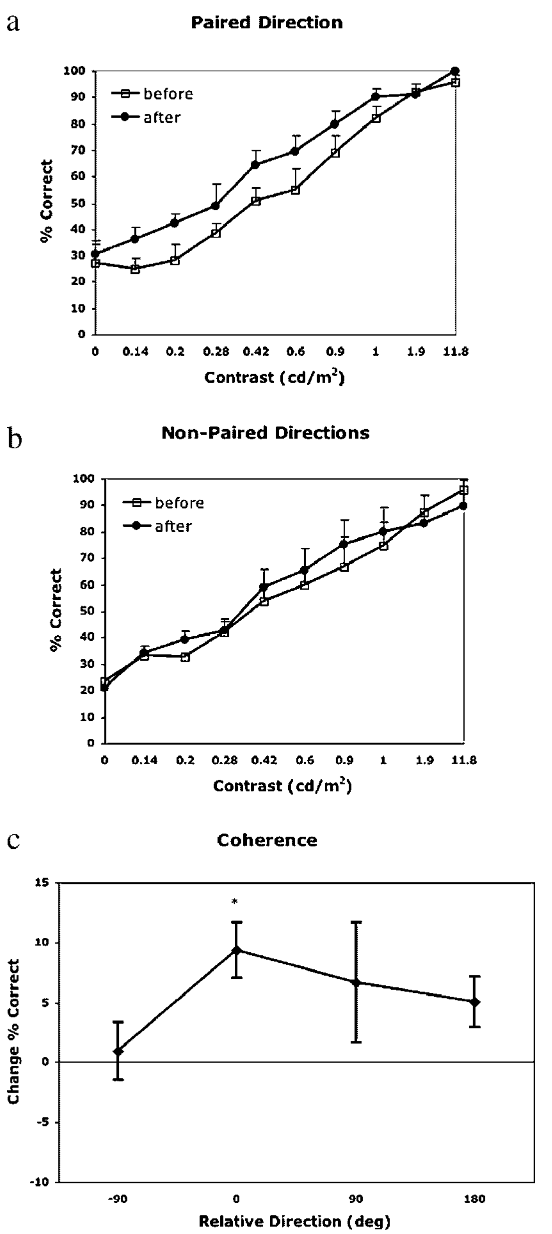

Figure 2. Motion sensitivity results. (a, b) Psychometric functions for paired and non-paired directions before and after learning. Contrast is the standard deviation of the mean luminance of the stimulus (Moulden *et al.*, 1990; Martinez-Trujillo and Treue, 2002) (see methods). To test for learning, a two-way ANOVA was run and showed significant improvement for the paired direction ($p < 0.001$), but not for the other directions ($p = 0.31$). (c) Coherence test results. The graph represents the percent of responses for each direction that were correct on the second test minus that on the first test aligned on the paired direction for each subject (0 is the paired direction). While significant learning was found for the paired direction ($p < 0.001$), no learning was found for other directions

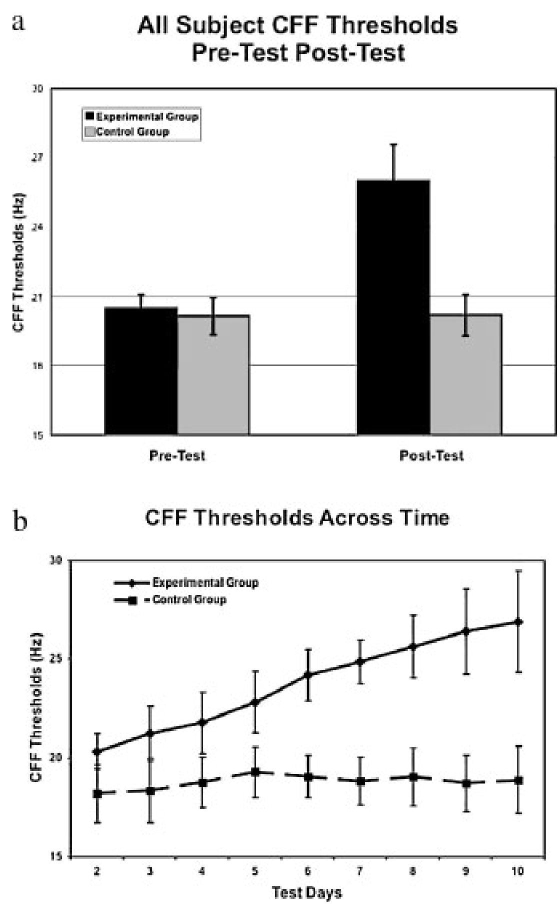

Figure 3. Critical flicker fusion (CFF) results. (a) Mean CFF thresholds for pre-tests and post-tests (in Hz) of all subjects. The experimental group showed a significant change between the pre- and post-test ($p < 0.0005$, *t*-test). (b) Mean CFF thresholds (in Hz) over time for experimental and control groups

The results of the CFF evaluations for the control subjects are shown in Figure 3. For control subjects, who conducted only tests of CFF, thresholds remained remarkably steady whether they were tested on the first and last day of the experiment (Figure 3a, grey bars) or if they were evaluated on multiple sequential days (Figure 3b, dashed line). This result was expected and corroborates those of previous studies (McClelland, 1987; Parkin *et al.*, 1997).

Surprisingly, CFF thresholds rose substantially in subjects who underwent the perceptual learning sessions. For these subjects the CFF threshold rose 30% between the first and last day of training (Figure 3a, solid bars) and this change was highly significant ($p < 0.0005$, *t*-test). In subjects whose CFF was evaluated daily (Figure 3b, solid line), a gradual, but dramatic, rise in CFF thresholds can be observed in subjects who underwent perceptual learning sessions.

DISCUSSION

Seitz and Watanabe (2003) proposed that during a cognitively demanding undertaking, such as the RSVP task, neuromodulators flood the brain, strengthening neural activity in a task-dependent manner. This concept is supported by studies showing that temporal pairing of sensory stimuli with electrical stimulation of areas releasing such neuromodulators results in an expanded cortical representation of neurons that respond to the paired stimuli (Kilgard and Merzenich, 1998; Bao *et al.*, 2001). In the current study, the increased CFF threshold may be a result of neuromodulators inadvertently strengthening neurons that are active, yet unrelated to the RSVP letter-identification task.

It is reasonable that CFF threshold changes accompany changes in motion processing abilities. The ability to process the speed of a stimulus is inexorably tied to the ability to process high temporal frequencies. Accordingly, neurones involved in motion processing respond to stimuli of higher temporal frequencies than those that best stimulate other visual areas (Priebe *et al.*, 2003).

The results show that the perceptual experience of subjects can dramatically alter CFF thresholds and should be an important consideration in the control of studies employing the CFF as a measure. Although our perceptual learning paradigm is rather specialized, it is likely that other visual experience of subjects could have similar effects. For instance, playing video games can induce a significant degree of visual learning (Green and Bavelier, 2003). While these authors did not examine CFF thresholds, subjects who played video games showed improvements on a variety of other visual tasks. Thus it is possible that changes to a subject's visual environment during the course of a research study can produce changes in CFF thresholds that are unrelated to the manipulations of that study. This should be a consideration in studies that employ CFF thresholds as a measure.

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