



Supramodal processing optimizes visual perceptual learning and plasticity



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ABSTRACT

Multisensory interactions are ubiquitous in cortex and it has been suggested that sensory cortices may be supramodal i.e. capable of functional selectivity irrespective of the sensory modality of inputs (Pascual-Leone and Hamilton, 2001; Renier et al., 2013; Ricciardi and Pietrini, 2011; Voss and Zatorre, 2012). Here, we asked whether learning to discriminate visual coherence could benefit from supramodal processing. To this end, three groups of participants were briefly trained to discriminate which of a red or green intermixed population of random-dot-kinematograms (RDKs) was most coherent in a visual display while being recorded with magnetoencephalography (MEG). During training, participants heard no sound (V), congruent acoustic textures (AV) or auditory noise (AVn); importantly, congruent acoustic textures shared the temporal statistics – i.e. coherence – of visual RDKs. After training, the AV group significantly outperformed participants trained in V and AVn although they were not aware of their progress. In pre- and post-training blocks, all participants were tested without sound and with the same set of RDKs. When contrasting MEG data collected in these experimental blocks, selective differences were observed in the dynamic pattern and the cortical loci responsive to visual RDKs. First and common to all three groups, vIPFC showed selectivity to the learned coherence levels whereas selectivity in visual motion area hMT+ was only seen for the AV group. Second and solely for the AV group, activity in multisensory cortices (mSTS, pSTS) correlated with post-training performances; additionally, the latencies of these effects suggested feedback from vIPFC to hMT+ possibly mediated by temporal cortices in AV and AVn groups. Altogether, we interpret our results in the context of the Reverse Hierarchy Theory of learning (Ahissar and Hochstein, 2004) in which supramodal processing optimizes visual perceptual learning by capitalizing on sensory-invariant representations – here, global coherence levels across sensory modalities.

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Introduction

Increasing evidence for multisensory integration throughout cortex has challenged the view that sensory systems are strictly independent (Driver and Spence, 2000; Ghazanfar and Schroeder, 2006), questioning in turn the innate specialization of sensory cortices. For instance early in development, auditory neurons can respond to light patches when rewired to receive visual information (Mao et al., 2011; Roe et al., 1990) and cooling specific parts of auditory cortex in deafened cats selectively perturbs the detection of visual motion and localization (Lomber et al., 2010). In congenitally blind humans, the cortical area hMT+ responsive to visual motion (human homolog of MT/V5 in

monkeys) is recycled for auditory or tactile processing (Bedny et al., 2010; Poirier et al., 2005; Ricciardi et al., 2007; Watkins et al., 2013) and the ventral and dorsal visual processing streams develop their functional specificity even when deprived of direct visual experience (Striem-Amit et al., 2012). Consistent with these observations, the “metamodal theory” (Pascual-Leone and Hamilton, 2001) and the “supramodal hypothesis” (Ricciardi and Pietrini, 2011; Voss and Zatorre, 2012) have suggested that some cortical areas may be naturally capable of functional selectivity irrespective of the sensory modality of inputs, hence of functional recycling. However, several questions have been raised (Bavelier and Hirshorn, 2010) among which: is functional recycling a consequence of sensory deprivation during a sensitive period or does it rely on pre-existing supramodal computational capabilities (Bedny et al., 2010; Dormal and Collignon, 2011; Morrone, 2010; Renier et al., 2013)?

In order to specifically address this issue, we trained non-sensory impaired individuals on a difficult and novel visual task and asked

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whether visual learning and plasticity would benefit from matched audiovisual stimulation. For this, three different groups of twelve individuals were recorded with magnetoencephalography (MEG) while they performed a visual discrimination task. MEG blocks consisted of a pre-training, a 20 minute individualized training and a post-training (Fig. 1A). It should be stressed that a short-training (20 min total) was used in all three training conditions; hence, we were interested in the possible effects of multisensory learning within a very short time period which may not match those obtained over days of training (e.g. (Shams and Seitz, 2008)). The main task consisted in determining which of a red or green intermixed population of random-dot-kinematograms (RDKs) was most coherent in the visual display (Fig. 1B); hence, this task implicated motion-color binding (what/where integration) and visual motion coherence discrimination. The pre- and post-training sessions were exclusively visual and tested the same RDK coherence levels for all three groups of participants; on the other hand, training sessions were individualized with regard to the RDK coherence levels and the training context. Specifically, participants could be trained in silence (V), with correlated acoustic textures (AV), or with auditory noise (AVn, control group). In the AV group, AV stimuli sharing redundant temporal regularities were designed using auditory analogs of visual RDKs i.e. acoustic textures (Overath et al., 2010) (Fig. 1C). In the control AVn group, the auditory stimulus was filtered noise. Both AV and AVn groups were told to neglect the sounds played in the background; in the AV group and unbeknownst to participants, the coherence of acoustic textures matched that of the target RDK (see Materials and methods, Fig. 1C).

Crucially, and for all participants, the RDK coherence levels were the sole criterion enabling to properly perform the task: first, the direction taken by the coherent dots was randomized across trials and orthogonal to the coherence level; second, acoustic textures could not inform on the color of the most coherent RDK albeit shared their dynamics;

third, acoustic textures were kept minimally accessible to participants' awareness. Additionally, all reported results exclusively focus on the comparison of pre- and post-training data in which no acoustic information was delivered to any of the participants (Fig. 1A): hence, we do not address the issue of multisensory integration per se (which takes place a priori during the training blocks) and instead focus on the effect of participants' training history on perceptual learning and cortical plasticity.

Materials and methods

Participants

All participants were right-handed, had normal hearing and normal or corrected-to-normal vision. Participants' ages ranged between 18 and 28 years old (mean age: 22.1 ± 2.2 s.d.). Prior to the study, participants were randomly split into three training groups, namely: an only visual training group (V, $n = 12$, 4 females), an audiovisual training group using acoustic textures (AV group, $n = 12$, 6 females) or using acoustic noise (AVn which is also a control group, $n = 12$, 6 females). Before the experiment, all participants provided a written informed consent in accordance with the Declaration of Helsinki (2008) and the local Ethics Committee on Human Research at NeuroSpin (Gif-sur-Yvette, France).

Experimental design

The magnetoencephalography (MEG) experiment was conducted in a darkened soundproof magnetic-shielded room (MSR). Participants were seated in upright position under the MEG dewar and faced a projection screen placed 90 cm away. We used a Panasonic DLP projector (model PT-D7700E-K, Panasonic Inc., Kadoma, Japan) with a refresh rate of 60 Hz. The sound pressure level was set at a comfortable hearing

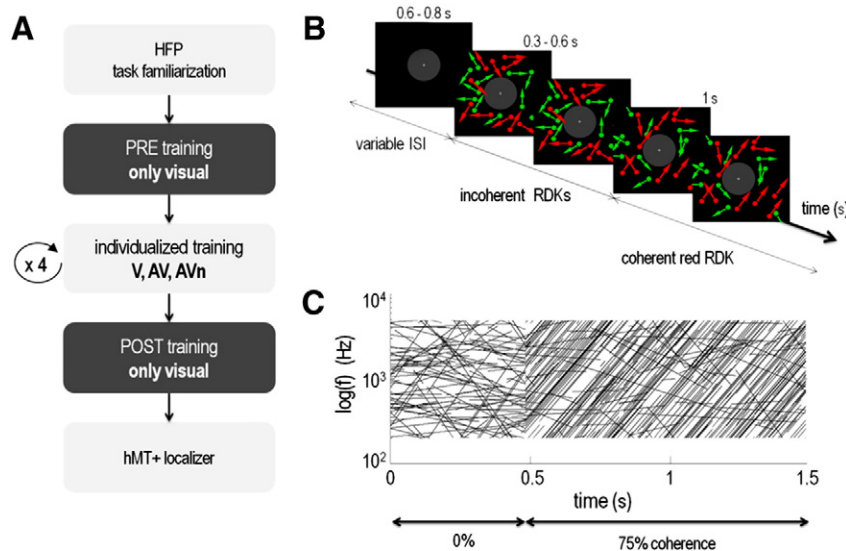


Fig. 1. Experimental design and stimuli. Panel A: an MEG session for one individual was composed of several blocks: first, the luminance of the red and green Random Dot Kinematograms (RDKs) was calibrated using Heterochromatic Flicker Photometry (HFP). Luminance calibration was followed by a few familiarization trials to the task during which participants received feedback. In the pre-training block, all participants were presented with stimuli that were solely visual. The pre-training data established the set of coherence levels for the training session based on an individual's coherence discrimination threshold. In the following four training blocks, participants were trained with four levels of RDK coherence. The four training blocks lasted 20 min and were without feedback. The training could be visual only (V), audiovisual using acoustic textures (AV) or audiovisual using acoustic noise (AVn). In the post-training block, each individual's coherence discrimination threshold was established with visual stimulation only. In the last block, a localizer provided an independent means to source localize the Human motion area hMT+ using combined functional MEG localizer data and anatomical MRI (see Materials and methods). Panel B: an experimental trial consisted in the presentation of a fixation cross followed by the appearance of two intermixed and incoherent RDKs (red and green populations). After 0.3 to 0.6 s, one of the two RDKs became more coherent than the other: the red RDK is here illustrated as the most coherent. Participants were asked to indicate which of the red or green population was most coherent irrespective of the direction of motion. Panel C: sample spectrogram in $\log(\text{frequency})$ as a function of time depicting an acoustic texture. By analogy to a visual RDK, the level of coherence in an acoustic texture was defined as the number of frequency ramps sharing the same slope in a given frequency range. Here, the spectrogram illustrates an incoherent acoustic texture lasting 500 ms followed by a 75% coherent acoustic texture lasting 1 s. Three groups of participants underwent three types of training. During V training, participants were solely provided with visual stimuli; during AV training, an acoustic texture was paired with the most coherent RDK population and the acoustic transition from incoherent to coherent was synchronized with the visual transition in the RDKs; during the AVn control training, the sound was a white noise unrelated to the visual RDKs. Inter-stimulus intervals were randomly drawn from 0.6 to 0.8 s. min = minutes; s = seconds; ms = milliseconds.

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