Motor Learning with Augmented Feedback: Modality-Dependent Behavioral and Neural Consequences

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Sensory information is critical to correct performance errors online during the execution of complex tasks and can be complemented by augmented feedback (FB). Here, 2 groups of participants acquired a new bimanual coordination pattern under different augmented FB conditions: 1) visual input reflecting coordination between the 2 hands and 2) auditory pacing integrating the timing of both hands into a single temporal structure. Behavioral findings revealed that the visual group became dependent on this augmented FB for performance, whereas the auditory group performed equally well with or without augmented FB by the end of practice. Functional magnetic resonance imaging (fMRI) results corroborated these behavioral findings: the visual group showed neural activity increases in sensory-specific areas during practice, supporting increased reliance on augmented FB. Conversely, the auditory group showed a neural activity decrease, specifically in areas associated with cognitive/sensory monitoring of motor task performance, supporting the development of a control mode that was less reliant on augmented FB sources. Finally, some remnants of brain activity in sensory-specific areas in the absence of augmented FB were found for the visual group only, illustrating ongoing reliance on these areas. These findings provide the first neural account for the "guidance hypothesis of information FB," extensively supported by behavioral research.

Keywords: audition, bimanual coordination, hMT/V5, motor learning, vision

Introduction

Behavioral scientists have long recognized that memory retrieval in humans and animals is influenced by the degree to which the context available at the time of retrieval corresponds with that present during initial training. A mismatch between initial encoding and subsequent retrieval can result in performance decrements (Tulving and Thomson 1973). Context can be defined broadly, including the external environment (information, instructional support, practice organization), as well as the internal state of the organism (mood state, motivation, etc.). One of the most striking demonstrations of this phenomenon has been that humans remember information better when tested in the same room as that in which the original learning occurred (Smith 1979).

Specific examples of this phenomenon are also abundant in motor skill learning. During skill acquisition, augmented feedback (FB) is often provided to boost performance. The term augmented refers to adding extrinsic FB (e.g., visual display of movement kinematics or kinetics) to the taskintrinsic FB that is normally available (e.g., normal vision or proprioception of the limbs) (Schmidt and Lee 2005). During the past decades, considerable evidence has been gathered, suggesting that providing augmented FB during training improves performance, whereas its removal during a subsequent test or retention condition may result in performance deterioration. This has come to be known as the "guidance hypothesis of information FB," suggesting that availability of augmented FB during training guides the learner toward proper performance, but its subsequent removal may lead to performance decrements (Salmoni et al. 1983; Schmidt et al. 1989, 1990; Winstein and Schmidt 1990; Swinnen 1996). This is presumably a consequence of the learner becoming dependent on augmented FB, possibly at the expense of relying on his/her own intrinsic sources of sensory information to support performance under nonaugmented test conditions (Salmoni et al. 1984; Swinnen 1996; Schmidt and Lee 2005; Magill 2007). Relatedly, the "specificity-of-learning hypothesis" implies that performance is optimal when acquisition and subsequent test conditions are similar in terms of available FB sources (Barnett et al. 1973; Proteau et al. 1987, 1992; Proteau 1992).

During the past decades, we have demonstrated that providing augmented visual FB also facilitates the learning of bimanual coordination patterns (Lee et al. 1995; Swinnen et al. 1997; Swinnen 2002; Debaere et al. 2003, 2004b; Puttemans et al. 2005), giving rise to complex multisensory integration mechanisms (Ronsse et al. 2009). However, as already indicated, the performer can become too dependent on augmented FB such that its subsequent removal results in performance deterioration and/or suboptimal long-term retention (Swinnen et al. 1997). Here, we explored a neural foundation for this dependence on augmented FB. Specifically, our working hypothesis was that FB dependence might be due to sustained reliance on sensory processing areas that have become tuned to this source of information during practice. To test this hypothesis, we investigated how the augmented sensory modality influences learning of a new bimanual pattern, corresponding to cyclical flexion/extension of both wrists, one being a quarter-cycle ahead of the other (90°-out-of-phase). Participants were randomly assigned to one of 2 groups, each receiving a different type of augmented FB: 1) One group received continuous visual FB by orthogonally plotting the displacement of the 2 hands into a single gestalt trajectory on the screen (a Lissajous figure with a circular formation) and 2) the other group received auditory FB at specific movement reversal landmarks, integrating the information from the 2 hands into a single temporal structure consisting of alternating high and low tones. By virtue of their nature, the auditory FB

Participants practiced the task during 5 sessions of 1 h, reaching a performance plateau. They were scanned using functional magnetic resonance imaging (fMRI) prior to and following practice of the skill to trace the practice-related neural signatures of skill acquisition. In particular, we hypothesized increased sensitivity to augmented FB processing with learning in the visual group, in line with previous findings (Debaere et al. 2004b; Puttemans et al. 2005). Such effects have not been documented in the literature for augmented auditory FB (e.g., see Coull et al. 2001). During the final scan session, performance was also tested without augmented FB to evaluate the degree of FB dependence in both groups. Here, we assessed remnants of augmented FB dependence in the form of sensoryspecific brain activations that could be linked with the unique sources of FB provided during training. This is possible because both FB modes were implemented according to different sensory modalities that were assumed to predominantly activate anatomically distinct areas. To the best of our knowledge, this is the first time that the neural foundation of the guidance hypothesis of augmented visual FB has been directly explored.

Materials and Methods

Participants

Thirty-eight adults (20 females, 18 males) aged between 20 and 30 (mean = 23) years were recruited from within the K.U.Leuven community. All were right handed as indicated by laterality quotients on the Edinburgh Handedness Inventory (Oldfield 1971). Participants were randomly distributed across 2 age- and gender-matched groups, who received different training protocols (see below). All were free of neuromuscular impairment at the time of testing and were not taking psychoactive or vasoactive medication. Informed consent was obtained, and participants were paid for participation. Procedures were conducted following guidelines established by the ethics committee of Biomedical Research at K.U.Leuven in compliance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Task Description and Procedure

Lying supine with forearms supported, participants produced cyclical flexion-extension movements with both wrists assuming sinusoidal trajectories. They were required to produce a 90°-out-of-phase coordination pattern, whereby one hand led the other by a quarter-cycle (Fig. 1*a*). This complex bimanual pattern requires intensive practice to be performed stably and consistently (Lee et al. 1995; Swinnen et al. 1997). In particular, it differs from intrinsic and naturally stable coordination modes (such as in-phase) because it requires a shift in the directional relation between both limbs 4 times per cycle (for an overview, see Swinnen 2002).

Both groups were involved in the same experimental procedures and differed only with respect to the mode of augmented sensory FB they received during bimanual coordination training, that is, visual (VIS) or auditory (AUD) FB (Fig. 1*b*). The AUD group practiced the required 90°-out-of-phase mode while receiving concurrent online auditory information by means of turning point pacing. Reversal points of the left and right hands were detected online from the kinematics (by means of peak detection algorithms) and were played back as low- and high-pitch tones, respectively, resulting in 4 equally spaced tones for each movement cycle when the task was performed correctly. At steady-state movement frequency, the rhythm of the 90°-out-of-phase pattern corresponded to regular alternation of both tones, resembling that of a galloping horse. Note that the AUD group heard this target template during about 15 s, at the beginning and in the middle of each

acquisition session, in order to facilitate the comparison of their own performance with this ideal template. The VIS group practiced the 90°-out-of-phase pattern while continuous online visual FB was provided by means of a Lissajous figure, displaying the left and right angular wrist displacement on the ordinate and abscissa, respectively (Fig. 1*b*). A cursor on the screen in front of the subject showed the orthogonal plot of both wrist displacements in real time, with the last 750 ms of the cursor trajectory remaining visible. When produced correctly, the 90°-out-ofphase pattern corresponded to a circular trajectory on the screen. Thus, in both groups, the augmented FB served to assist bimanual movement production: the ideal template for the VIS group was a circular configuration on the screen, whereas the AUD group aimed to produce a distinct temporal structure of alternating high and low tones, associated with the 90°-out-of-phase pattern.

Across all days, participants also performed an in-phase bimanual movement pattern (repeated simultaneous flexion followed by extension of both wrists, 10 trials per day). This pattern is intrinsic to the motor repertoire (Zanone and Kelso 1992; Kelso 1995; Swinnen 2002) and thus represents a control condition not requiring learning. Accordingly, since this condition was not exposed to augmented FB, it was expected that it would not exhibit reliance on specific sensory processing areas during the skill acquisition and retention phases. Participants were instructed to move at their preferred amplitude and frequency and to preserve these parameters across the different coordination modes (in-phase and 90°-out-of-phase) and sessions. The tasks only differed from each other with respect to the phase offset between both limbs, which was 0° for the in-phase and 90° for the training task.

Subjects were instructed to move both wrists continuously throughout each trial. Forearm-hand orthoses restricted movements to wrist flexion-extension and prevented compensation from adjacent joints. Angular displacements were registered by means of non-ferromagnetic high-precision shaft encoders (HP, 2048 pulses per revolution, sampling frequency 100 Hz), fixed to the movement axes of both orthoses. The interface recording the orthoses position, providing online augmented FB (either auditory or visual), and synchronizing with the scanner (when applicable) was programmed with Labview (National Instruments).

Subjects underwent 2 scanning sessions: before (day 0) and after (day 5) training, see Figure 1c. The training sessions (days 1, 2, 3, and 4) took place in a dummy scanner, closely mimicking the experimental context of the actual scanner, including reproduction of the scanner noise.

Training

All subjects practiced the 90°-out-of-phase pattern with the help of augmented FB (either AUD or VIS), performing 8 blocks containing 10 trials of bimanual movement (duration = 21 s per trial) each day across 4 training days. Previous learning studies involving similar coordination patterns, showed that such a training regime resulted in skilled performance and stable error scores by the end of training, as evidenced by a performance plateau (Debaere et al. 2004b; Puttemans et al. 2005; Ronsse et al. 2009). These blocks were preceded by a single block (10 trials, 21 s per trial) in which participants had to perform the intrinsic in-phase pattern, receiving no augmented FB. Moreover, subjects performed the 90°-out-of-phase without augmented FB during a single block (10 trials, 21 s per trial) at the end of day 4. Short rest periods were offered to the subjects in the middle of and in between each block.

Scanning

Scanning occurred before (day 0, PRE) and after (day 5, POST) training (see Fig. 1*c*). The following conditions were administered during PREscanning: 1) performance of the 90°-out-of-phase task with augmented FB (FB_90°), that is, visual information for the VIS group and auditory information mode without augmented FB (NO_FB_IN), and (3) rest without any information presented (REST). During POST-scanning, conditions were 1) FB_90°, 2) performance of the 90°-out-of-phase task without augmented FB (NO_FB_0°), and 4) REST. The condition order was randomized. Each scanning condition lasted 21 s and was symbolically cued on the screen, remaining visible for 3 s.



Figure 1. Experimental set up and protocol. (*a*) Target movement: the performer had to continuously move both wrists back-and-forth, maintaining a 90°-out-of-phase (a quarter of the cycle) relationship between effectors. (*b*) Ideal trajectory of both wrists across time. Augmented FB to the VIS group was provided by displaying the position of both wrists as the orthogonal coordinates of a single cursor. Perfect 90°-out-of-phase cyclical movement corresponded to a circular trajectory on the screen. Augmented FB to the AUD group was provided by delivering a low tone (*b* symbol) when the left hand reached either maximum flexion or maximum extension, and a high tone (*k* symbol) when the right hand reached either maximum flexion or regular alternation of both tones. (*c*) Experimental protocol. The daily experimental session was divided into several blocks/runs. Before training (day 0), subject performed the new pattern (90°-out-of-phase) with augmented FB (either AUD or VIS) as well as the control in-phase pattern (without augmented FB) in the scanner. On days 1, 2, 3, and 4, participants performed first the control in-phase movement (one block, without augmented FB), then 8 blocks of the 90°-out-of-phase pattern with augmented FB. Participants further performed this new pattern without augmented FB during one block on day 4. On day 5, participant went back to the scanner to perform the in-phase pattern (without augmented FB. and the 90°-out-of-phase pattern with augmented FB. and the 90°-out-of-phase pattern without augmented FB. The runs actually executed in the fMRI scanner (shaded gray) also included "REST" epochs (no movement).

Subjects were instructed to switch conditions as soon as this template appeared. To avoid eye movements across conditions, subjects were instructed to keep their eyes open at all times and to fixate a cross projected in the middle of their visual field during each condition. To prevent carry over effects between the different tasks, a short rest period (3 s) was added whenever 2 movement conditions succeeded one another immediately. A bite bar was used to minimize movements of the head, and a mirror was utilized to allow vision of images projected onto a screen mounted above the shoulders. This setup prevented subjects from seeing their hands during the movement task. Subjects wore headphones for communication with the experimenter and for hearing the movement-driven pacing tones (AUD group).

Image acquisition was achieved using a Siemens 3 T Magnetom Trio MRI scanner (Siemens) with standard head coil. Each PRE-scanning session included a high-resolution T_1 -weighted image (magnetization prepared rapid gradient echo; time repetition [TR] = 2300 ms, time echo [TE] = 2.98 ms, 1 × 1 × 1.1 mm voxels, field of view [FOV]: 240 × 256, 160 sagittal slices) for anatomical detail. fMRI data were acquired over 3 time series (i.e., runs) with an interleaved echo planar imaging (EPI) pulse sequence for T_2^* -weighted images (TR = 3000 ms, TE = 30 ms, flip angle = 90°, 50 oblique slices each 2.8 mm thick, interslice gap 0.028 mm, in-plane resolution 2.5 × 2.5 mm, 80 × 80 matrix). Three scans at the beginning of each run were discarded from analysis to

allow for scanner equilibration. Each of the 3 runs lasted 354 s (5.9 min) in PRE-scanning and 474 s (7.9 min) in POST-scanning, consisting of 5 blocks of each condition (21 s per block, i.e., 7-whole-brain images).

Kinematic Data Analyses

Peak-to-peak amplitude values were calculated per cycle and averaged within and across hands and trials for each of the different conditions. Similarly, the movement frequency was calculated, that is, the number of complete movement cycles per second. Movement period was computed as the inverse of frequency.

Coordinative ability was determined using the relative phase (ϕ) between left and right wrists, as calculated according to the following formula (Ronsse et al. 2009):

$$\phi = \arctan\left(\frac{\theta_r \dot{\theta}_l - \theta_l \dot{\theta}_r}{\frac{\dot{\theta}_r \dot{\theta}_l}{2\pi f} + 2\pi \bar{f} \theta_r \theta_l}\right),\tag{1}$$

where θ_r , $\dot{\theta}_r$, θ_l , and $\dot{\theta}_l$ denote the position and velocity of the right and left wrists, and \bar{f} is the mean movement frequency over the corresponding trial. The mean and standard deviation (SD) of ϕ over

a trial were calculated according to circular statistics standards (e.g., Fisher 1983):

$$\mu_{\phi} = \arg\left(\int_{0}^{T} e^{i\phi(t)} dt\right), \tag{2}$$

$$\sigma_{\phi} = \sqrt{-2\ln \left\| \frac{\int_{0}^{T} e^{i\phi(t)} dt}{T} \right\|},\tag{3}$$

where *T* is the trial duration. We further computed the absolute deviations of μ_{ϕ} from the target relative phase (i.e., 90° for the 90°-out-of-phase pattern and 0° for the in-phase pattern) as a measure of relative phase accuracy. The SD (σ_{ϕ}) of relative phase estimated movement pattern stability. All parameters were determined for each trial and subsequently averaged across repetitions and blocks/runs.

Kinematic Variables were analyzed with Multifactorial Analysis of Variance:

- A 2 × 6 analysis of variance (ANOVA) was conducted on the data corresponding to the FB_90° condition, to quantify learning effects (supposed to be visible as an exponential decrease of both the absolute deviations of μ_{ϕ} from the target relative phase—the average absolute error [AE] for short—and the SD σ_{ϕ}), and potential differences across groups. The factors were thus group (AUD and VIS) and day (0-PRE, 1, 2, 3, 4, and 5-POST).
- Similarly, a 2 × 6 (group × day) ANOVA was conducted on the data corresponding to the NO_FB_IN condition, to establish whether performance changes occurred in this control condition.
- A 2 × 2 × 2 (group × scan day × movement mode) ANOVA was conducted on the kinematic data obtained during scanning to reveal potential differences in movement amplitude and/or periodicity across group and time for the FB_90° and NO_FB_IN movement conditions.
- Most importantly, a 2 × 2 (group × augmented FB condition) ANOVA was conducted on the POST-training kinematic data obtained during scanning; comparing each groups performance of the 90°-out-ofphase pattern with and without augmented FB. This enabled assessment of the impact of FB removal on movement accuracy and stability.

Statistical significance was considered at P < 0.01. Post hoc analyses were performed using Tukey's honestly significant difference test.

fMRI Data Analyses

Imaging data were processed using Statistical Parametric Mapping (SPM) 5 software (Wellcome Department of Imaging Neuroscience) implemented in MatLab 7.6 (R2008a) (MathWorks). For each subject, EPI volumes were realigned to the first image in the first PRE time series and a mean image was created from the realigned volumes. Due to excessive head movements during scanning, 4 subjects were removed from the analyses (1 female and 1 male in AUD group and 2 males in VIS group), such that the reported analyses finally focused on the data of 17 subjects per group. In the remaining subjects, an "unwarp" procedure was applied to the realigned images to extract unwanted movement-related variance independent of variance related to the task conditions (Andersson et al. 2001). The images belonging to 1 subject (female, VIS group)-which presented only a few very short and transient head movements up to 4 mm-were further corrected using the "ArtRepair" toolbox (Mazaika et al. 2005): movement threshold 1 mm/TR, of 804 EPI's, 4.5% repaired, and 16.4% deweighted in firstlevel model. No significant differences were found when comparing analyses in which this subject was included or removed. Normalization of the resulting images was performed using a standardized EPI template based on the Montreal Neurological Institute reference brain in Talairach space (Talairach and Tournoux 1988). Voxels were subsampled at 2.5 × 2.5 × 2.5 mm and smoothed with a Gaussian kernel (10 mm full-width half-maximum).

All statistical analyses were performed in accordance with the general linear model (Friston et al. 1995). A covariate of no interest was specified to remove brain activity due to visual cueing of the conditions (same onsets as the visual cues, 1 TR duration). For conditions of interest, boxcar functions representing periods of FB_90° (PRE/POST), NO FB 90° (POST only), and NO FB IN (PRE/POST) movement were modeled (duration 6 TRs). All regressors were convolved with the canonical hemodynamic response function provided in SPM 5 and subjected to high-pass filtering (1/138 Hz for PRE scans, 1/186 Hz for POST scans) to remove low-frequency drifts. Conditions of interest were contrasted against REST for each individual and then subjected to second-level, random-effects ANOVAs with the factors group (AUD/ VIS), scanning time (PRE/POST), and task (FB_90°/NO_FB_90°/ NO FB IN). We further investigated the practice-related changes (PRE/POST) in the FB 90° condition for each group separately since we discovered different performance characteristics depending on the augmented FB mode.

For the majority of analyses, a voxelwise threshold of P < 0.05 with a false discovery rate (FDR) correction for multiple comparison was utilized. Only clusters with an extent of at least 15 voxels were considered. Analyses conducted with different thresholds are explicitly specified in the text.

Results

Kinematic Data

The kinematic data illustrated a clear improvement of the 90°out-of-phase pattern across practice for both the AE, that is, absolute deviation of the relative phase between hands (μ_{ϕ}) from the target relative phase (Fig. 2*a*), and SD (σ_{ϕ} , Fig. 2*b*). ANOVA reached significance for AE with $F_{5,192} = 20.5$ (P < 0.0001) and for SD with $F_{5,192} = 24.2$ (P < 0.0001), with practice day as factor. Moreover, the analysis of AE revealed a significant group effect ($F_{1,192} = 26.4, P < 0.0001$), showing that the VIS group performed better on average. However, post hoc tests revealed that the 2 groups started and ended at comparable performance levels during the PRE- and POST-test, respectively (all P > 0.99). As such, the group effect was primarily driven by performance differences during the acquisition phase. The group effect on SD and the interaction effect on AE and SD did not reach significance. In contrast, no changes for in-phase performance were found since the corresponding ANOVAs did not reach significance across groups, days, or their interaction.

Elimination of the augmented FB strongly affected performance of the VIS group but not the AUD group. A 2 \times 2 (group × augmented FB condition) ANOVA was conducted on the POST-training scanning runs, including the FB 90° and NO_FB_90° data. Importantly, for AE (Fig. 2a), the main effect of FB condition reached significance ($F_{1,64} = 9.8, P < 0.003$), and there was a group × FB condition interaction ($F_{1,64} = 9, P <$ 0.004). Post hoc Tukey's tests further confirmed that both groups finally reached the same performance level when augmented FB was available but that the AE of the VIS group during the condition without augmented FB was significantly higher than in the remaining 3 conditions (all P < 0.005). This suggests that the VIS group was highly dependent on augmented FB for successful performance, showing significant AE increases when this source of information was removed, whereas the AUD group largely preserved performance in the absence of augmented FB. The same analysis on the SD (Fig. 2b) reached significance for the main effect of condition, albeit just above the 0.01 threshold ($F_{1,64} = 6.4, P < 0.02$), with performance being less stable when the augmented FB was



Figure 2. Kinematic data: these panels report the evolution across days of relevant kinematic parameters. (a) Absolute deviation of the mean relative phase between hands (μ_f) from the target relative phase (AE), and (b) SD (σ_{Φ}) of relative phase between hands. The red lines refer to the 90°-out-of-phase pattern with augmented FB (FB_90°), the blue lines refer to the 90°-out-of-phase pattern without augmented FB (NO_FB_90°), only executed at the end of training (days 4 and 5); the black lines refer to the in-phase pattern without augmented FB (NO_FB_90°), only executed at the end of training (days 4 and 5); the black lines refer to the in-phase pattern without augmented FB (NO_FB_90°), only executed at VIS (solid lines) groups. The error bars represent the between-subjects standard error.

removed. Post hoc pairwise comparisons did not reach significance.

Amplitude and cycle period remained largely similar across groups and conditions (Supplementary Fig. S1). Only one group difference was found such that the VIS group executed the 90°-out-of-phase pattern with larger amplitude than the AUD group over the whole practice period (2 × 6 ANOVA, $F_{1,192}$ = 13.3, P < 0.0004).

In sum, the kinematic data showed strong FB dependence for the VIS group, while the AUD group performed equally well with or without augmented FB at the end of the learning phase. This suggests that the 2 groups were substantially different in terms of their acquired capability to perform under nonaugmented FB conditions.

Imaging Data

First, we established the brain networks that were activated by both groups when performing the FB_90° condition during the PRE and POST scans. The 2 groups strongly activated the structures that are usually involved in the production of coordinated movements, that is, bilateral sensorimotor cortices, the supplementary motor area (SMA), and cerebellum. Additionally, the AUD group activated the thalamus and auditory processing areas, including temporal cortex and rolandic operculum, while the VIS group activated areas typically involved in visual processing, such as the bilateral occipital cortices.

We built an inclusive mask from the union of these 4 conditions (AUD + PRE, AUD + POST, VIS + PRE, or VIS + POST) for the subsequent analyses, such that any voxel/cluster that was active in at least one of the 4 conditions was included (Friston et al. 2006). These areas are shown in Supplementary Figure S2 and listed in Supplementary Tables S1 (AUD) and S2 (VIS).

Practice-Specific Changes in Brain Activity during 90°-Out-of-Phase Movement with Augmented FB

The practice-related changes in activity for movement production with augmented FB (FB_90° condition) were investigated with a 2×2 ANOVA design, with group (AUD/

VIS) as first factor and scan time (PRE/POST) as second factor.

Main effect of group. As expected, group differences in brain activation were predominantly found in bilateral areas responsive to visual and auditory input (Fig. 3): the VIS > AUD contrast revealed occipital areas extending to middle temporal (MT) areas and superior parietal lobules, while the AUD > VIS contrast revealed activation in primarily temporal and opercular areas. In addition, the AUD > VIS contrast also revealed cerebellar areas (bilateral lobule VIII and vermis X), right SMA, left precentral gyrus, and bilateral inferior frontal gyri.

Main effect of time. Both decreases (PRE > POST) and increases (POST > PRE) in brain activation across practice were identified (see Table 1). Many cortical areas decreased activity with practice, including sensorimotor, (pre)frontal, temporal, and parietal areas. As will be shown below, these changes appeared primarily driven by the AUD group. In contrast, a single area showed a practice-related increase in activity, that is, the right superior occipital gyrus. This effect appeared primarily driven by changes in the VIS group, as discussed next.

Group-specific practice-related changes. Because of the different nature of augmented FB provided to each group, and the consistent differences revealed in the kinematics, we explored practice-related changes for the AUD and VIS group separately. For the AUD group, many areas showed a significant decrease in activity from PRE to POST, as shown in Figure. 4a and listed in Table 2. Most of these areas actually overlapped with those identified for the main effect of time discussed previously (PRE > POST, see Table 1), consisting of bilateral sensorimotor areas and SMAs, opercular, temporal, and parietal areas. This test also revealed 2 prefrontal areas that were more activated during the initial phase of learning, that is, the right middle orbital gyrus and the right middle frontal gyrus. More specifically, the cluster identified as the right middle frontal gyrus corresponds to Brodmann area 46, part of the



Figure 3. Localization of areas showing more activation for the AUD (AUD > VIS) and VIS (VIS > AUD) group when executing the 90°-out-of-phase pattern, overlaid on a standard Montreal Neurological Institute template brain. Bar plots represent blood oxygen level-dependent responses for the activated areas during the PRE (plain) and POST (hatched) scans for the AUD (yellow) and VIS (cyan) groups. All P < 0.05 after correction for FDR. L, left; R, right.

Table 1

Areas with significant practice-related decrease (PRE > POST) or increase (POST > PRE) for the 2 groups combined, during the execution of the FB_90° condition

Brain region	Side	Significant effect	Peak activation coordinate (Montreal Neurological Institute)			BA	T value
			Х	Y	Ζ		
Primary sensory and (pre)motor cortex							
Postcentral gyrus	L	PRE > POST	-50	-33	63	BA 1/2	3.69
Superior frontal gyrus	R	PRE > POST	15	0	68	BA 6	4.48
Middle orbital gyrus	R	PRE > POST	30	50	-13	BA 11	3.89
Middle frontal gyrus (DLPFC)	R	PRE > POST	43	43	25	BA 45	3.36
Occipital cortex							
Superior occipital gyrus Temporal cortex	R	POST > PRE	20	-103	18	BA 17	5.5
Middle temporal avrus	L	PRE > POST	-58	-68	3	BA 37	3.94
Temporal pole Parietal cortex	R	PRE>POST	60	18	-8	BA 38	3.67
Superior parietal lobule	R	PRE > POST	50	-35	58	BA 1	4.21
Supramarginal gyrus	L	PRE > POST	-65	-28	23	BA 48	3.61

Note: L, left; R, right; BA, Brodmann area. These comparison tests reached P < 0.05 after correction for FDR.

dorsolateral prefrontal cortex (DLPFC). Interestingly, no brain areas became significantly more active across practice for the AUD group.

In contrast, some areas showed increased activity for the VIS group as learning progressed, namely in the bilateral occipital gyri (the left side also encompassed the lingual gyrus) and cerebellar lobules IV-V and VI and vermis IV-V and VIII (Fig. 4*b* and Table 3). There were no brain areas for the VIS group in which activation decreased across practice. We further calculated a group × time interaction, which confirmed the above results but appeared significant only at an uncorrected level (P < 0.01), see Supplementary Table S3.

Remnants of Augmented FB: Differences in Brain Activation When Performing the Learned Movement under Nonaugmented FB Conditions

A central question in the present study was to determine differences in brain activation between both groups following training when deprived of augmented FB, that is, during the NO_FB_90° condition at POST. Any difference between both groups would thus be a result of the earlier practice context. Conversely, such an effect was not expected during the



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Figure 4. Localization of areas showing practice-related changes when executing the 90°-out-of-phase pattern, overlaid on a standard Montreal Neurological Institute template brain. (a) Activation decrease (PRE > POST) for the AUD group. (b) Activation increase (POST > PRE) for the VIS group. Insets represent blood oxygen level-dependent response changes across practice for the AUD (yellow) and VIS (cyan) groups. All P < 0.05 after correction for FDR. L, left; R, right.

NO_FB_IN condition because the in-phase coordination mode was never performed in the presence of augmented FB. With respect to the 90°-out-of-phase mode, the kinematic data already revealed a dependence on FB for the VIS group, performing much worse without than with augmented FB. In contrast, the AUD group largely preserved performance when augmented FB was removed.

To assess brain activation differences between both groups, a 2 × 3 (group × movement condition) ANOVA was applied to the POST-training data. The factor movement condition consisted of 3 levels: FB_90°, NO_FB_90°, and NO_FB_IN. A constrained search (Friston et al. 2006) was performed using a mask (thresholded at P < 0.01, FDR corrected) that preserved only the voxels showing significant differences between groups in the FB_90° condition (i.e., 90°-out-of-phase with FB, see Fig. 3). This mask was used in order to focus on the (predominantly sensory specific) areas that were different across groups in the condition with augmented FB. The FB_90° and NO_FB_IN conditions were incorporated in the design in order to determine whether the observed differences in the NO_FB_90° were actually inherited from or unique to the learned movement (FB_90°) or whether it was also apparent during performance of the intrinsic coordination mode (NO_FB_IN).

Within the ANOVA model, planned group comparisons for the NO_FB_90° were performed (AUD > VIS and VIS > AUD *t*tests). Even though both groups performed the task without augmented FB under exactly the same conditions, the VIS group exhibited more activation than the AUD group bilaterally in the occipitotemporal cortex (at the boundary between BA 19 and BA 37, see Fig. 5). This part of the occipitotemporal Areas with significant practice-related decrease (PRE > POST) for the AUD group, during the execution of the FB_90° condition

Brain region	Side	Peak activation coordinate (Montreal Neurological Institute)			BA	T value
		Х	Y	Ζ	-	
Primary sensory and (pre)motor cortex						
Postcentral gyrus	R L	38 43	-45 -43	73 68	BA 1/2 BA 1/2	3.52 4.17
Supplementary motor area Superior frontal gyrus	R	15	0	68	BA 6	4 4 9
	L	-10	-10	63	BA 6	3.27
Middle orbital gyrus Middle frontal gyrus	R R	28 30	53 45	-13 25	BA 11 BA 46	4.29 3.33
(DLPPC) Inferior frontal gyrus (pars opercularis)	R	48	13	18	BA 44	3.59
Inferior frontal gyrus (pars triangularis)	R	43	28	8	BA 45	3.14
Opercular area						
Rolandic operculum	R L	53 —60	-18 8	18 0	BA 48 BA 44	3.10 3.23
Temporal cortex						
Superior temporal gyrus	R L	70 —43	-33 3	20 	BA 22 BA 48	2.52 2.41
Temporal pole Parietal cortex	R	63	15	-5	BA 38	4.23
Supramarginal gyrus	R L	60 63	-30 -28	33 23	BA 2 BA 48	3.38 4.17
Superior parietal lobule	R L	38 	-58 -45	68 78	BA 7 BA 1	3.20 3.29
Inferior parietal lobule	R L	33 —53	-38 -28	50 43	BA 2 BA 2	2.36 3.02

Note: L, left; R, right; BA, Brodmann area. These comparison tests reached P < 0.05 after correction for FDR.

Table 3

Areas with significant practice-related increase (POST > PRE) for the VIS group, during the execution of the FB 90° condition

Brain region	Side	Peak activation coordinate (Montreal Neurological Institute)			BA	T value
		Х	Y	Ζ	_	
Occipital cortex						
Superior occipital gyrus	R	18	-100	20	BA 18	4.50
Middle occipital gyrus	L	-13	-98	3	BA 17	3.35
Calcarine gyrus	R	13	-95	3	BA 17	4.17
Lingual gyrus	L	-13	-90	-10	BA 18	3.49
Cerebellum						
Lobule IV-V	R	15	-48	-15		3.60
Lobule VI	R	10	-65	-23		3.26
Vermis IV-V	_	0	-55	-15		3.77
Vermis VIII	_	5	-68	-40		3.73

Note: L, left; R, right; BA, Brodmann area. These comparison tests reached P < 0.05 after correction for FDR.

cortex, also known as hMT/V5+, is the human homologue of the monkey MT/V5 complex (Zeki et al. 1991; Watson et al. 1993; Tootell et al. 1995; Tootell and Taylor 1995) and plays a central role in the perception of visual motion (Zihl et al. 1983, 1991; Zeki 1991; Debaere et al. 2003). As shown in the bar plots, the VIS group (cyan, solid bars) activated hMT/V5+ when (visual) FB was available, whereas the AUD group (yellow, solid bars) exhibited a deactivation of this area (FB_90° condition). Interestingly, this group difference remained even when the task was performed without augmented FB (NO_FB_90° condition) even though the VIS



Figure 5. Localization of areas showing more activation for the VIS as compared with the AUD group (VIS > AUD) when executing the 90°-out-of-phase pattern without augmented FB (NO_FB_90°), overlaid on a standard Montreal Neurological Institute template brain. All P < 0.05 after correction for FDR. L, left; R, right. Bar plots represent blood oxygen level-dependent responses for the activated areas during the FB_90° (plain), NO_FB_90° (hatched), and NO_FB_IN (empty) trials for the AUD (yellow) and VIS (cyan) groups. Asteriks emphasize significant pairwise comparisons at P < 0.05, FDR corrected (**) and P < 0.001, uncorrected (*).

group activated hMT/V5+ to a smaller extent during the latter condition. By contrast, no group difference was found when the in-phase task (NO_FB_IN condition) was performed without augmented FB, even when a very liberal threshold was applied (P < 0.05 uncorrected).

Surprisingly, the VIS group also exhibited more activation of the auditory cortex relative to the AUD group (Fig. 5). However, this effect was driven by a strong deactivation in the AUD group when the task was performed without FB. A similar deactivation was evident for the NO_FB_IN condition and statistics revealed a trend toward significance for the right hemisphere (P < 0.001, uncorrected). Several studies have shown that increases in cerebral blood flow in task-relevant sensory cortical areas are often accompanied by decreases in other task-irrelevant sensory areas, for example, visual cortex during auditory tasks (Haxby et al. 1994; Kawashima et al. 1995; Lewis et al. 2000; Laurienti et al. 2002), an effect that is potentially visible here as well.

Discussion

In the present article, we investigated how augmented FB influences learning of a new bimanual pattern. Our behavioral results showed that subjects who practiced with visual FB (VIS group) acquired the new bimanual coordination pattern successfully, but performance deteriorated significantly when the augmented FB was removed at the end of training. Conversely, subjects practicing the same task with auditory FB (AUD group) showed less progress at initiation of practice but eventually reached the same performance level as the VIS group. Interestingly, the AUD group preserved its performance level when external FB was removed. Thus, in line with previous behavioral findings, our results established that the VIS group became dependent on the augmented FB and used this information to trigger corrective actions. In contrast, the

AUD group performed equally well with or without augmented FB, suggesting that this group adopted a control strategy, which gradually became more independent of the augmented FB as practice progressed. Similar modality-specific behavioral effects were obtained during acquisition and subsequent retention of a tracking task (Coull et al. 2001).

Our imaging results further corroborated these behavioral findings in that the 2 training regimes induced changes within differential neural pathways, as illustrated by a global decrease of tempero-parieto-frontal areas for the AUD group and an increase of vision/sensorimotor-specific areas for the VIS group. The novel finding is that the VIS training regime resulted in activation of the visual motion area hMT/V5+ even when augmented FB was no longer provided (i.e., no visual stimuli were presented). By contrast, the group that trained with the auditory sensory modality exhibited a deactivation of task-specific sensory areas during the no-FB condition.

Brain Activation and Practice-Related Changes Specific for Each Training Regime

When augmented FB was available, the VIS group activated dorsal visual stream areas that process visual information to guide movements in space (see also Debaere et al. 2003, 2004a, 2004b; Puttemans et al. 2005). The (extra) striate regions within the occipital cortex are connected to the parietal cortex (Boussaoud et al. 1990), which in turn is reciprocally connected to the premotor regions (Cavada and Goldman-Rakic 1989; Kurata 1991), playing a major role in visuomotor transformations (Sakata and Taira 1994; Jeannerod et al. 1995; Clower et al. 1996; Kalaska et al. 1997; Rushworth et al. 1997; Rizzolatti et al. 1998; Buneo et al. 2002). Moreover, activity in the cerebellum increased in the VIS group after training, falling mainly into the primary sensorimotor zone, as identified by O'Reilly et al. (2010). In sum, the visual (and perhaps also some of the cerebellar) areas, exhibiting higher activity in the VIS group after training, reflected the performer's increased tuning to the augmented visual FB to steer behavior.

The AUD group showed activity in a broad network responsive to auditory and proprioceptive information. The superior temporal areas (BA22), temporal pole (BA38), and inferior frontal gyrus (BA 44) are involved in auditory processing (e.g., Callan et al. 2003; Wang et al. 2003; Seung et al. 2005; Zarate and Zatorre 2008), particularly in the context of motor control (e.g., Lahav et al. 2007). Right BA22 plays a fundamental role in nonverbal sound processing (Bernal et al. 2004). SMA is strongly activated by explicit timing tasks, especially when the pattern is generated internally (Rao et al. 1997; Debaere et al. 2003). Moreover, SMA is also activated during the processing of proprioceptive information (Naito et al. 2005; Hagura et al. 2009). Both aspects were strongly required to perform the complex 90°-out-of-phase coordination pattern, and our result is in excellent agreement with previous studies that identified high SMA activation when rhythmical coordination tasks were executed (Sadato et al. 1997; Stephan et al. 1999; Jäncke et al. 2000; Immisch et al. 2001; Toyokura et al. 2002; Ullén et al. 2003; Debaere et al. 2004a; Goble et al. 2010).

Another apparent difference between both groups is that the AUD group showed high involvement of prefrontal areas, for example, the right middle orbital gyrus (BA11) and the right middle frontal gyrus, with the latter corresponding to the DLPFC (BA 46). DLPFC is often activated during initial stages of

learning and has consistently been associated with "attention to action." When performance becomes more automatic, attention demands are reduced and DLPFC activation decreases (Toni et al. 2001, 2002; Debaere et al. 2004b). On the other hand, the medial areas of orbitofrontal cortex appear to be involved in ongoing monitoring of the reward value of various reinforcers (Kringelbach and Rolls 2004), such as sounds or music (Blood et al. 1999; Frey et al. 2000). In sum, DLPFC and orbitofrontal cortex are generic brain areas involved in many tasks (including those that are cognitive in nature), illustrating the important role of cognition in action control (Andersen and Cui 2009). That DLPFC together with orbitofrontal cortex was particularly active in the AUD group at the start of practice may be related to the fact that this group may have been faced with the more cognitively demanding task of assessing the difference between the obtained augmented FB and the ideal auditory template held in working memory. Moreover, the successful preservation of performance at the end of practice suggests that this information was used to gradually elaborate an "internal controller," possibly based on feedforward control. This computational process appeared to be no longer necessary once the controller was acquired at later stages of practice. This suggests a role for prefrontal cortex in generation of predictions by presensitizing the relevant movement representations to process incoming auditory FB rapidly during initial practice. Interestingly, such proactive generation of predictions has also been associated with orbitofrontal cortex activation in research on visual recognition (Bar 2007). In any case, the more elaborate prefrontal activations in the AUD group suggest a stronger cognitive involvement in learning the coordination task.

The differential evolution of brain activations associated with augmented VIS versus AUD FB requires further consideration. Even though one would in principle expect a similar tuning to, and dependence on augmented FB, irrespective of the mode of sensory information, it is noteworthy that behavioral evidence for such FB dependence has been extensively documented for concurrent visual, but not auditory FB (Swinnen 1996; Coull et al. 2001). Moreover, the AUD FB group in the present study also failed to show this FB dependence and associated brain activation pattern. Several reasons can be advanced for the obtained differential effect. With respect to the VIS group, it is likely that the augmented FB was so powerful that it became the principal source of sensory information, at the expense of proprioceptive processing. This made performance under removal of augmented visual FB vulnerable because proprioception is the only source of sensory information left to guide performance under these circumstances. For the AUD group, subjects may have ignored the FB from the very start of practice, but this is unlikely because the present task is difficult if not impossible to learn in the absence of any source of augmented FB (see also Kovacs et al. 2010). Moreover, the extensive temperofrontal activations at pretest do not appear to support refusal to process auditory FB. Alternatively, the AUD FB may have been less salient in guiding performance online due to its temporal nature. This may have created a more challenging learning environment, encouraging subjects to gradually rely more on processing of proprioceptive information. Indeed, steering corrective actions based on proprioceptive FB may have been more difficult at the start of practice since no "ideal" proprioceptive template, against which actual sensory information could be compared, was available to the

participants. In fact, proprioceptive templates of the preexisting (intrinsic) in-phase and anti-phase patterns could have even interfered with acquisition of the 90°-out-of-phase task. Therefore, it is reasonable to assume that, early in learning, proprioceptive information was closely monitored and mapped onto the auditory augmented FB, which served as confirmation of the required movement pattern. The principal auditory information processing areas were shown to decrease activity with practice in the AUD group. Further research is required to determine the generalizability of the obtained differential augmented FB effects on skill acquisition.

Activation Patterns during Performance in the Absence of Augmented FB

Brain activation networks in the absence of augmented FB (NO_FB_90°) were directly compared between both groups during the POST scan (i.e., after the training session). Even though both groups performed exactly the same task under the same conditions, the VIS but not the AUD group activated hMT/V5+ (note that no visual or auditory input was provided). Moreover, hMT/V5+ responded strongly to the VIS FB_90° condition, underscoring its specificity to the visual information provided during training. It is also particularly noteworthy that hMT/V5+ was not active during the NO_FB_IN condition, indicating that it was only activated in association with the practiced 90°-out-of-phase motor task.

We postulate that the visual training regime resulted in strong visuomotor associations that were specific to both the provided augmented FB and the practiced motor task. Consequently, hMT/V5+ was still activated in the absence of augmented sensory input, presumably because subjects internally reconstructed (imagined) the missing visual FB (Slotnick et al. 2005; Kaas et al. 2010). Alternatively, the persistent activations may have been a consequence of enhanced interactions among visual and (higher order) sensorimotor areas within the trained network, such that task-specific motor activity was sufficient to coactivate hMT/ V5+. Similarly, McIntosh et al. (1998) showed that learning an association between auditory and visual stimuli can elicit neural activation of visually specific areas when presenting the auditory cue only. By contrast, sensory areas specifically engaged by our AUD training regime were deactivated when the task was performed without FB, indicating that they were not part of the motor representation of the 90°-out-of-phase pattern.

Differential Control Strategies Associated with Different Sensory Modalities

Extending previous findings, the present behavioral and brain imaging data revealed that the VIS group acquired the new bimanual pattern by adapting a controller that strongly depended on the presence of augmented FB, such that 1) learning was associated with increased activation of visual as well as sensorimotor areas, 2) performance dropped significantly when the augmented visual FB was withdrawn, and 3) the visual motion area hMT/V5+ remained activated even without visual input, but only when the learned 90°-out-ofphase task was performed. By contrast, the AUD group acquired the same coordination pattern by gradually becoming independent of the augmented FB, as suggested by our behavioral and functional imaging results. It is tempting to speculate that the AUD group relied more strongly on an internal controller based on proprioceptive FB and/or direct feedforward control, depending less on the augmented FB loop. Altogether, the behavioral and brain imaging data provide a highly convergent picture about the association between degree of dependence on augmented FB during learning and performance deterioration during subsequent weaning from augmented FB.

The implications of the present findings are 2-fold. First, it appears that augmented information FB may become part of the neural representation of movement, consistent with the guidance hypothesis of information FB (Salmoni et al. 1984) or specificity-of-learning hypothesis (Barnett et al. 1973; Proteau et al. 1987, 1992; Proteau 1992). This hypothesis implies that performance is optimal when the test conditions (available FB sources) match closely with the context afforded during practice. A change in the context may lead to performance deterioration. This may equally apply to settings in which natural as well as augmented information FB sources, change from training to test contexts (Barnett et al. 1973; Proteau et al. 1987, 1992; Proteau 1992). Even though the impact of context alterations between motor training and test conditions has been documented extensively during the past decades, to our best knowledge, this is the first time that a comprehensive neural account of this behavioral phenomenon is provided.

Second, some types of augmented FB may give a strong boost to performance during skill acquisition but may also create some dependence on this FB source. This has important practical consequences for training and rehabilitation because these are intended to promote generalizability of learning across various contexts and to facilitate a patient's functional independence in natural (nonaugmented FB) environments. It is, therefore, of critical importance to maximally exploit the benefits of augmented FB while reducing or eliminating its negative consequences. One possibility is to optimally prepare the learner/patient for future performance conditions without augmented FB, that is, through progressive weaning from augmented FB (Winstein and Schmidt 1990). After all, we teach skills not only to perform optimally in the training or rehabilitation setting but also in the real world.

Summary and Conclusions

The present study provided a highly convergent picture between behavioral performance and brain activation during the acquisition phase with and subsequent performance without augmented FB. Our data provide the first direct neural account for the extensively supported "guidance hypothesis of information FB" with respect to the visual modality, predicting that a learner can benefit from augmented FB to boost performance but can also become too dependent on augmented FB such that its subsequent removal results in performance deterioration and/or poor retention (Salmoni et al. 1984; Swinnen 1996; Schmidt and Lee 2005; Magill 2007). We suggest a neural account, whereby the visual information becomes an integral part of the sensorimotor representation via practice, resulting in an augmented FB-dependent controller. This is supported by the remnants of activation in visual processing areas following the removal of augmented FB and, presumably, insufficient reliance on proprioceptive FB sources. In contrast, the group receiving auditory FB developed a control strategy that was apparently more independent from the presence of augmented FB. Consistent with this account is

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the preserved performance of the AUD group when weaned from augmented FB. These findings have important consequences for organization of practice in rehabilitation settings. The key will be to find the right balance between exploiting the benefits associated with augmented FB, while at the same time alleviating a performer's dependence on it.

Supplementary Material

Supplementary Figures S1 and S2 and tables S1-S3 can be found at: http://www.cercor.oxfordjournals.org/

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