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Performed or observed keyboard actions affect pianists' judgements of relative pitch

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Action can affect visual perception if the action's expected sensory effects resemble a concurrent unstable or deviant event. To determine whether action can also change auditory perception, participants were required to play pairs of octave-ambiguous tones by pressing successive keys on a piano or computer keyboard and to judge whether each pitch interval was rising or falling. Both pianists and nonpianist musicians gave significantly more "rising" responses when the order of key presses was left-to-right than when it was right-to-left, in accord with the pitch mapping of the piano. However, the effect was much larger in pianists. Pianists showed a similarly large effect when they passively observed the experimenter pressing keys on a piano keyboard, as long as the keyboard faced the participant. The results suggest that acquired action–effect associations can affect auditory perceptual judgement.

Keywords: Action; Pitch perception; Action observation; Internal models; Prediction; Tritone paradox.

It is widely recognized that perception is important for action because it specifies the environment within which a movement is taking place and provides sensory feedback during and after the movement. Reciprocal effects of action on perception, however, are less well established and still have the ring of novelty. Interest in such effects has been awakened in recent years by *common coding theory* (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1990), which postulates that actions are represented in terms of the sensory effects they are expected to produce, and by the related theory of internal models (Jordan & Rumelhart, 1992; Kawato, 1999; Miall & Wolpert, 1996; Wolpert & Kawato, 1998), according to which *forward models* automatically generate sensory predictions during an action and compare those predictions with the actual sensory input. When the sensory input is ambiguous, the forward model's predictions could shift

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perception of sensory input in the predicted direction.

One elegant demonstration of such an effect is due to Wohlschläger (2000). He presented participants with circular visual arrays resembling a clock face that could be perceived as rotating in either a clockwise or an anticlockwise direction. While observing such stimuli, participants were required to turn a knob in a clockwise or anticlockwise direction according to a visual cue (an arrow), with their hand being hidden from view. The direction of the manual action significantly biased the reported direction of rotation of the visual display. A similar bias was observed when participants merely pressed a left or right key in response to the cue (left and right are strongly associated with anticlockwise and clockwise, respectively) and even when they delayed the planned key press until after they had judged the visual stimulus. Because the two directions of rotation were unambiguous and mutually exclusive (i.e., the stimuli were perceptually bistable), the effect was most likely perceptual and not due to a response bias induced by the actions. In other words, it seems that the manual action really made participants see the display differently.

Many studies have since found specific effects of action on visual perception (Casile & Giese, 2006; Grosjean, Zwickel, & Prinz, 2009; Hamilton, Wolpert, & Frith, 2004; Jacobs & Shiffrar, 2005; Jordan & Hunsinger, 2008; Maruya, Yang, & Blake, 2007; Miall et al., 2006; Sack, Lindner, & Linden, 2007; Schubö, Aschersleben, & Prinz, 2001; Symes, Tucker, Ellis, Vainio, & Ottoboni, 2008; Vishton et al., 2007; Wühr & Müsseler, 2001; see Schütz-Bosbach & Prinz, 2007, for a review), as well as on the perceived timing of visual or auditory stimuli that were contingent on the action (Haggard & Clark, 2003; Haggard, Clark, & Kalogeras, 2002; Ichikawa & Masakura, 2006; López-Moliner & Linares, 2006). For example, Haggard et al. (2002) found that a tone that was contingent on a key press but occurred after a short delay was perceived as occurring closer in time to the action (and vice versa) than when the action was a finger twitch elicited involuntarily by magnetic brain stimulation. However, there was no reason to expect any effect of these manipulations on the way the tones sounded to the participants.

Can actions affect auditory perception?

Few studies have investigated potential effects of action on the perception of specifically auditory stimulus attributes such as pitch, loudness, or timbre. Phillips-Silver and Trainor (2007) found that rhythmic movement biases adult participants' interpretation of a metrically ambiguous auditory rhythm as being in either duple or triple meter, having shown previously that infants' perception of the same rhythm can be similarly influenced by bouncing them in synchrony with it (Phillips-Silver & Trainor, 2005). However, this effect is likely to be one of perceptual organization, not of perceived changes in relative loudness or duration of the sounds. In another study, Sams, Möttönen, and Sihvonen (2005) showed that silent mouthing of syllables can alter the perception of different, concurrently presented syllables. This effect on speech perception is smaller than the effect of visually observing another speaker's incongruent lip movements (McGurk & MacDonald, 1976). It could reflect changes in auditory perception or in phonetic categorization, or both. Indeed, action may have effects at different levels of perception and cognition, and recent theorizing and research suggest that that the separation between these levels is much less clear-cut than was previously thought (Barsalou, 2008; Fischer & Zwaan, 2008; Glenberg & Kaschak, 2002, 2003; Spivey, 2007).

In order for actions to affect auditory perception, strong links between them must exist. This is the case in expert musicians. The associations of particular action features with particular sound features that are formed in the course of learning to play a musical instrument are probably the strongest that exist outside of the speech domain. For example, skilled pianists have heard millions of tones contingent on their manual actions on a keyboard. Unlike many other musical instruments, piano keyboards have a simple pitch mapping: The pitch of tones increases monotonically from left to right. Pianists thus acquire particular action–effect mappings that do not exist in other people including nonpianist musicians such as violinists and flautists.

That there is a strong coupling between keyboard actions and their perceptual consequences in pianists has been confirmed in research showing effects of irrelevant musical sounds on the speed and accuracy of keyboard actions (Drost, Rieger, Brass, Gunter, & Prinz, 2005a, 2005b; Drost, Rieger, & Prinz, 2007). Importantly, pianists were affected only by sounds that can be produced on a keyboard (piano or organ sounds), whereas guitarists were sensitive only to guitar sounds (Drost et al., 2007). Mikumo (1994, 1998) showed that spatially distributed actions (finger tapping or visuomotor tracking) can facilitate or interfere with pianists' memory for melodies, depending on whether they are congruent or incongruent with the familiar left-to-right pitch mapping. Recent research in neuroscience has provided impressive evidence for shared auditory and motor processing networks in pianists and other musicians (Bangert & Altenmüller, 2003; Bangert, Jürgens, Häusler, & Altenmüller, 2006a; Bangert et al., 2006b; Baumann et al., 2007; D'Ausilio, Altenmüller, Olivetti Belardinelli, & Lotze, 2006; Hasegawa et al., 2004; Haslinger et al., 2005; Haueisen & Knösche, 2001; Lahav, Saltzman, & Schlaug, 2007; Mutschler et al., 2007; Zatorre, Chen, & Penhune, 2007). This functional overlap may be what enables pianists to recognize their own performances when they hear them played back after a delay of several months (Keller, Knoblich, & Repp, 2007; Repp & Knoblich, 2004).

Of particular interest here is a study by Bangert et al. (2006a) in which pianists and nonmusicians were trained to exhibit conditioned eye-blink responses to tones that were initially accompanied by air puffs to the eye. Subsequently, the participants were required to depress silent piano keys, and the pianists (but not the nonmusicians) tended to exhibit eye-twitch responses at the moment of key depression. One plausible interpretation of this finding is that the pianists automatically generated an auditory image of a tone when they depressed a piano key. This would be consistent with the automatic operation of an internal forward model that predicts the sensory consequences of the keyboard action.

Perception of octave-ambiguous tone pairs

In our research we asked whether the direction of hand movement when pressing two successive keys on a silent keyboard affects judgements of the relative pitch height of octave-ambiguous tones that are triggered by the key presses. In particular, we predicted that pianists will more often judge the pitch interval between the tones as ascending when they move from left to right (L–R) on the keyboard than when they produce exactly the same tones by moving from right to left (R–L). Such a result might imply that pianists' pitch perception is influenced by how they normally produce tones on their instrument. Given the strong evidence for shared auditory and motor processing networks in pianists, such an influence could easily reflect a modulation of perception by predictions generated by an internal forward model. By contrast, musicians who play nonkeyboard instruments should show such an effect to a lesser extent or not at all.

We borrowed the stimulus materials from research on the *tritone paradox* (Deutsch, 1986, 1987, 1991; Deutsch, Kuyper, & Fisher, 1987). They comprise 12 tone pairs whose first tone represents one of the 12 chromatic pitch classes (semitone steps within an octave), whereas the second tone always differs from the first by an interval of a tritone (six semitones, or half an octave). The individual tones are composed of octave-spaced partials whose relative amplitudes are governed by a fixed envelope function, so that all tones are equal in average pitch height (Shepard, 1964). Because of the inherent octave ambiguity of such tones, each tone pair can in theory be perceived as either ascending or descending in pitch. In other words, these stimuli are perceptually bistable, like the rotating visual displays used by Wohlschläger (2000), for which they constitute a kind of auditory analogue. In practice, however, individuals tend to perceive some pairs predominantly as ascending and others as descending, and these may differ from individual to individual, so that it is necessary to present the complete set of 12 pairs in any experiment. Only the pairs located at the category boundaries are truly bistable.

We report two experiments that address the effects of keyboard actions on pianists' perception of such tritone pairs. The purpose of Experiment 1 was to establish whether pianists indeed hear tritone intervals more often as ascending when they press keys in a L–R sequence than when they press them in a R–L sequence. For the sake of simplicity we call this the action direction effect (ADE). In Experiment 2 we investigated whether an ADE is obtained when pianists merely observe another person pressing the keys that produce the ambiguous tone pairs and whether the orientation of the keyboard matters.

EXPERIMENT 1

In this experiment we compared two groups of participants: pianists and nonpianist musicians.[1] If pianists show an ADE, and if that effect is caused by internal predictions based entirely on extensive sensorimotor experience with piano keyboards, then nonpianists should not show the effect. However, to the extent that the pianists' ADE is not due to the specific sensorimotor links that they have acquired between actions and auditory effects, but is due to other factors, such as the explicit knowledge of how pitch is mapped onto a piano keyboard, then other musicians should show an ADE as well because they have similar knowledge. If both sensorimotor links and general knowledge play a role, then pianists should show a larger ADE than nonpianists.

Two recent stimulus–response compatibility studies involving simple response keys (Lidji, Kolinsky, Lochy, & Morais, 2007; Rusconi, Kwan, Giordano, Umiltà, & Butterworth, 2006) have found evidence for an association between the horizontal spatial dimension and pitch height in musicians, but not in nonmusicians. The effect did not depend on piano expertise and thus seemed to be cognitive in nature. Moreover, even though Lidji and colleagues called the effect "a piano in the head", the knowledge was generalized because a piano keyboard was not needed to evoke the association. Therefore, we also addressed the question of whether the ADE in musicians depends on the use of a piano keyboard by including a condition in which pianists and nonpianists pressed horizontally separated keys on a computer keyboard to produce the tones.

If the ADE in pianists reflects their extensive sensorimotor experience with piano keyboards, then it should be smaller on a computer keyboard than on a piano keyboard. However, it should not disappear completely because the directional aspect of the movement remains the same and because the key-press actions required on the two keyboards are similar in this study. If the ADE reflects merely a general association between the horizontal dimension and pitch height in musicians (Lidji et al., 2007; Rusconi et al., 2006), it should not depend on the keyboard used. Because nonpianist musicians have little sensorimotor experience with piano keyboards, they should not show a difference between the two keyboard conditions.

Method

Participants

Twenty-four Yale undergraduates (ages 18–21 years) served as paid participants. All were classically trained musicians who had studied their primary instruments since an early age and played at an advanced level. Twelve (5 women) were pianists, and the other 12 (8 women) were nonpianists (violin—4, viola—2, cello—5, clarinet—1). Of the nonpianists, 4 had had limited piano training (less than two years, the stated criterion for

[1] We reported the results for pianists previously in a brief research note that did not contain any methodological detail (Repp & Knoblich, 2007). There we contrasted the pianists' performance with that of an unselected and therefore somewhat heterogeneous group of Rutgers University undergraduates, who showed no significant ADE. Here we present data obtained from a different, perhaps more appropriate, comparison group.

participation) in the distant past; the other 8 had no piano training at all.

Materials

The stimuli were 12 octave-ambiguous tones representing the 12 chromatic pitch classes (semitone steps) within an octave. The tones were synthesized online by a program written in MAX/MSP (Version 4.0.9) [Available from http://www.cycling74.com] according to specifications in Deutsch et al. (1987). Each tone consisted of six octave-spaced partials whose relative amplitudes were governed by a fixed convex spectral envelope function centred on C4 (262 Hz). Thus, even though the tones represented different pitch classes, they had the same average pitch height and were, therefore, ambiguous with regard to the octave they represented.

From the 12 individual tones, 12 pairs were formed, such that each pair started with a different pitch class and spanned the interval of a tritone (6 semitones). These 12 pairs were arranged into 12 different semirandom orders (blocks), constructed so that across the 12 blocks each pair followed each other pair once. Each block was then expanded to twice its length by appending the 12 pairs in reverse order. Half of the first 12 pairs in each block were randomly assigned to the L–R direction on the keyboard, and the other half was assigned to the R–L direction. The corresponding pairs in the second half of each block were given the opposite assignment. Thus, in each block of 24 pairs, each of the 12 pairs appeared with both the L–R and the R–L action directions.

The mappings of the tones to the keys on the (silent) piano and computer keyboards are listed in Table 1. On the piano keyboard, each tone was mapped to a key representing its pitch class. The keys used encompassed the range from A#2 (MIDI pitch 46) to D#4 (MIDI pitch 63). Because octave-ambiguous tones are invariant under octave transposition, keys an octave apart (e.g., MIDI pitches 46 and 58) produced exactly the same tone. A paper strip displaying numeric labels was mounted above the piano keys. The numbers were either ascending or descending from left to right, to control for any potential effect of the number labels themselves on pitch

Table 1. *Mapping of tone pairs to piano and computer keys*

Tone pairs (Pitch classes)		*Piano keys (MIDI pitches)*		*Computer keys (Letters)*	
A#	E	46	52	W	Y
B	F	47	53	R	I
C	F#	48	54	Y	P
C#	G	49	55	D	J
D	G#	50	56	G	L
D#	A	51	57	X	N
E	A#	52	58	E	U
F	B	53	59	T	O
F#	C	54	60	S	H
G	C#	55	61	F	K
G#	D	56	62	Z	B
A	D#	57	63	C	M

Note: Movement from left to right on each keyboard is shown; right-to-left movement has the reverse order.

judgements. The condition with ascending numbers used the actual MIDI pitch numbers, as shown in Table 1. In the condition with descending numbers, the same mapping from tones to keys was employed, but the key labels were reversed on the paper strip (i.e., subtracted from 109). The horizontal separation of piano keys for a tritone pair ranged from 7 cm (F–B) to 9.5 cm (B–F). In the computer keyboard condition, the mapping of pitches to keys was less systematic, due in part to the two-dimensional layout of the computer keyboard. However, the keys for a tritone pair were always in the same row of the computer keyboard and had three other keys in between; their horizontal separation was 7.5 cm.

Design and equipment

The experiment was controlled by programs written in MAX/MSP 4.0.9 running on an iMac G4 computer, and participants listened over Sennheiser HD540II earphones. The piano keyboard was a three-octave Fatar Studio 37 MIDI controller, connected to the computer via a MIDI translator. Playback was set to a comfortable level. Each participant in each group performed in both a piano keyboard and a computer keyboard condition within a single session of about 75 minutes duration. Half of the participants started with one condition, and the other half started with the other condition. Within each of these orders, one half performed the piano keyboard condition with ascending key labels, and the other half performed it with descending key labels.

Procedure

Participants sat in front of the computer monitor that displayed pairs of prompts (numbers in the piano keyboard condition, letters in the computer keyboard condition), with the labels FIRST and SECOND printed above them. The participants' task, illustrated in a few practice trials, was to press the corresponding keys in the proper succession using the index finger of their preferred hand and to judge whether the pitch went up or down between the two tones.[2] Pressing the keys with the index finger was expected to be equally easy for pianists and nonpianists on both the piano and the computer keyboards, and it required horizontal movement of the arm, which may be important with regard to the ADE (though this hypothesis was not tested in the present study). Depression of a key produced a tone for as long as the key was held down. Pressing other keys by mistake did not result in any sound. The pitch judgement response was given on the computer keyboard, using the up-arrow key for "up" (a rising pitch interval) and the down-arrow key for "down" (a falling pitch interval). A forced choice was required. After a response was given, the next pair of prompts appeared on the screen.

In the piano keyboard condition, the MIDI controller was placed in front of the participant, and the computer keyboard was pushed to the right side. A tone pair could be played repeatedly before giving a response, but participants rarely used this option because frequent use would have extended the duration of the session considerably.[3] After each block of 24 trials, there was a brief pause during which the data were saved, and the next block was selected. Participants were encouraged to work at a comfortable but not too slow pace. Each keyboard condition ($12 \times 24 = 288$ tone pairs) typically took about 30 minutes to complete.

Results

For each participant, the ADE was calculated by subtracting the overall percentage of "up" responses to tone pairs played with R–L key presses from the overall percentage for the same tone pairs played with L–R key presses. (This is equivalent to subtracting the percentage of "down" responses to tone pairs played with L–R key presses from the percentage for tone pairs played with R–L key presses.) A positive percentage thus represents the predicted ADE. Figure 1 shows the group means with standard errors for the two keyboard conditions. A significant ADE was observed in each case, $t(11) = 3.72$, 3.45, 4.49, and 3.64, respectively, all $ps < .01$. There were large individual differences among pianists, which are reflected in the standard error bars. Nonpianists showed less individual variability.

A mixed-model analysis of variance (ANOVA) with the between-participant variables of group, order of keyboard conditions, and labelling of piano keys (treated as a dummy variable for the computer keyboard condition), and the within-participant variable of keyboard condition was conducted on the individual ADE scores. The only significant effect was the main effect of

[2] The handedness of participants was not recorded, but there were no more than one or two left-handers in each group, and even they may have used their right hand. For pianists, the hand used to press the keys should not matter because the pitch mapping is the same for both hands. For players of string instruments, whose left hand regulates pitch, there might possibly be a larger ADE for the left than for the right hand, but this effect may not be in the horizontal direction (cf. Mikumo, 1998) and may not be exhibited at all when pressing keys on a keyboard. Such possible instrument-specific effects were not investigated in the present study.

[3] One pianist was an exception; he took almost 2 hours for the session. His ADE was slightly below the average for the pianist group. All other participants completed the session within about 75 minutes.

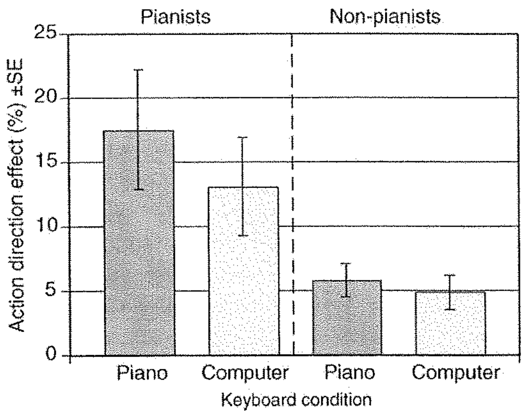

Figure 1. *Overall results of Experiment 1: The action direction effect (percentage difference in "up" responses to tone pairs played with left-to-right vs. right-to-left key presses on a keyboard) in two groups of participants, with standard error bars.*

group, $F(1, 16) = 5.43$, $p = .03$: The ADE was significantly larger for pianists than for nonpianists. The main effect of keyboard did not reach significance, $F(1, 16) = 3.15$, $p = .10$, and the Group × Keyboard interaction was not significant either, $F(1, 16) = 1.36$, $p = .26$. Nevertheless, it should be noted that pianists showed a tendency towards a larger ADE with the piano keyboard than with the computer keyboard, and this tendency did reach significance in a separate *t*-test, $t(11) = 2.24$, $p < .05$. Nonpianists showed little difference between the keyboard conditions.

The instrument played by the nonpianists did not seem to play a role. The 5 cellists showed a mean ADE (across both keyboard conditions) of 5.6%, whereas the 5 violinists and 1 violist showed a mean effect of 5.3%. Moreover, the 4 nonpianists who had had some piano instruction long ago did not show a larger effect than the others who had never touched a piano (4.6% vs. 5.7%).

The fact that there were no other significant effects in the ANOVA further implies that neither the order of keyboard conditions nor the labelling of the piano keys played any role. In particular, both the Order × Keyboard interaction, $F(1, 16) = 2.73$, $p = .12$, and the Labels × Keyboard interaction, $F(1, 16) = 0.07$, $p = .79$, were nonsignificant.

Discussion

The results of Experiment 1 provide evidence that actions can affect the perceptual judgement of an auditory stimulus attribute that is strongly associated with the actions. When participants pressed two keys in a L–R order to hear a pair of octave-ambiguous tones, they were more likely to judge the tritone interval between the tones as ascending (and less likely to judge it as descending) than when they pressed the keys in a R–L order. The significantly larger ADE in pianists than in nonpianists who had equally extensive musical training can only be attributed to the pianists' extensive sensorimotor experience with piano keyboards. The small but nevertheless significant ADE in nonpianists may reflect an influence of knowledge about keyboards or a general association of pitch height with the horizontal dimension (Lidji et al., 2007; Rusconi et al., 2006), or possibly a weak sensorimotor link acquired through observation of pianists in action.

The way the keys on the piano keyboard were labelled (ascending vs. descending numbers) did not have any effect. This was important to demonstrate because numerous studies of the so-called SNARC (spatial numeric associations of response codes) effect, where reaction time is the dependent variable, have shown that numbers are conceptualized as increasing from left to right (e.g., Dehaene, Bossini, & Giraux, 1993; Gevers, Verguts, Reynvoet, Caessens, & Fias, 2006; Restle, 1970; Schwarz & Keus, 2004; however, see also Santens & Gevers, 2008). It would seem natural to associate this horizontal "number line" with pitch height when pitch varies along the horizontal dimension. However, such spatial–numerical associations evidently played no role in the present paradigm, perhaps because the numbers were much larger than the single-digit numbers that are typically used in studies of the SNARC effect.

The order of the two keyboard conditions also did not matter. This suggests that the ADE on the computer keyboard was not due to carry-over from a preceding piano keyboard condition. When starting the experiment, half the participants did not yet know that they would later use a piano keyboard, yet they showed an ADE on the computer keyboard. Pianists did show a somewhat larger ADE on the computer keyboard when that condition followed the piano keyboard condition than when it preceded it (15.6% vs. 10.6%). Nonpianists instead tended to show a larger ADE in whichever condition came second (6.7% vs. 4.0%). These tendencies might reach significance in a larger sample.

EXPERIMENT 2

Experiment 2 focused on pianists and addressed two new questions. First, would an ADE be obtained if pianists merely observed another person pressing keys on a piano keyboard? Many recent studies have demonstrated that action observation engages the neural systems that are involved in action execution (for reviews, see Jeannerod, 2006; Knoblich, 2008; Rizzolatti & Craighero, 2004). As long as the observed action is in the observer's repertoire, his or her action system "resonates" to it, which amounts to an internal simulation and a tendency to perform the action (which, however, is normally inhibited). Given this functional overlap of action execution and action observation, our expectation was that an ADE would also be found in a passive observation condition.

The second question addressed by Experiment 2 was whether the orientation of the piano keyboard would matter. What would happen if the keyboard were turned around, so that it is facing away from the pianist? This manipulation dissociates two factors that are perfectly correlated in pianists' training: the direction in which the pianist's hand moves and the pitch mapping of the instrument. Recently, it has been shown that humans form specific internal models for combinations of particular types of actions and particular tools (Imamizu et al., 2000; Imamizu, Kuroda, Miyauchi, Yoshioka, & Kawato, 2003; Imamizu, Kuroda, Yoshioka, & Kawato, 2004; see also Daprati & Sirigu, 2006). If a reversed keyboard becomes an unfamiliar "tool", the ADE may be significantly reduced or even eliminated. The same should be true in a passive observation condition, at least if pianists use the same internal models in action execution and in action observation (Wilson & Knoblich, 2005).

Method

Participants

Twelve skilled pianists (9 Yale undergraduates and 3 graduate students from the Yale School of Music; ages 18–24 years; 5 women) were paid for their participation. Three of the undergraduates had participated in Experiment 1, but about one year had elapsed since.

Materials, design, and equipment

Materials were the same as those in Experiment 1. The design was a within-participant 2 × 2 factorial, with the two variables being action condition (active or passive) and keyboard orientation (normal or reversed). The order of action conditions was counterbalanced: Half the participants started with the active condition and half with the passive condition. Within each action condition, half the participants started with the normal keyboard orientation (facing the participant), and the other half started with the reversed orientation (facing away from the participant). Each action condition used the same 12 blocks of 24 tritone pairs each: 6 blocks with the normal keyboard orientation and 6 blocks with the reversed orientation. Inspection of the data of Experiment 1 had suggested that a reliable ADE could be obtained with 6 blocks of trials.

The equipment was the same as that in Experiment 1, except for two differences. First, the strip of descending number labels was affixed to the back of the MIDI controller, while simultaneously the ascending labels were mounted above the keys. In other words, the key labels (whose direction had had no effect in Experiment 1) remained fixed in this experiment and were seen as reversed when the orientation of the piano keyboard was reversed (see Figure 2). Second, the tones were played not over headphones but through a pair of Macintosh transparent "eyeball" loudspeakers

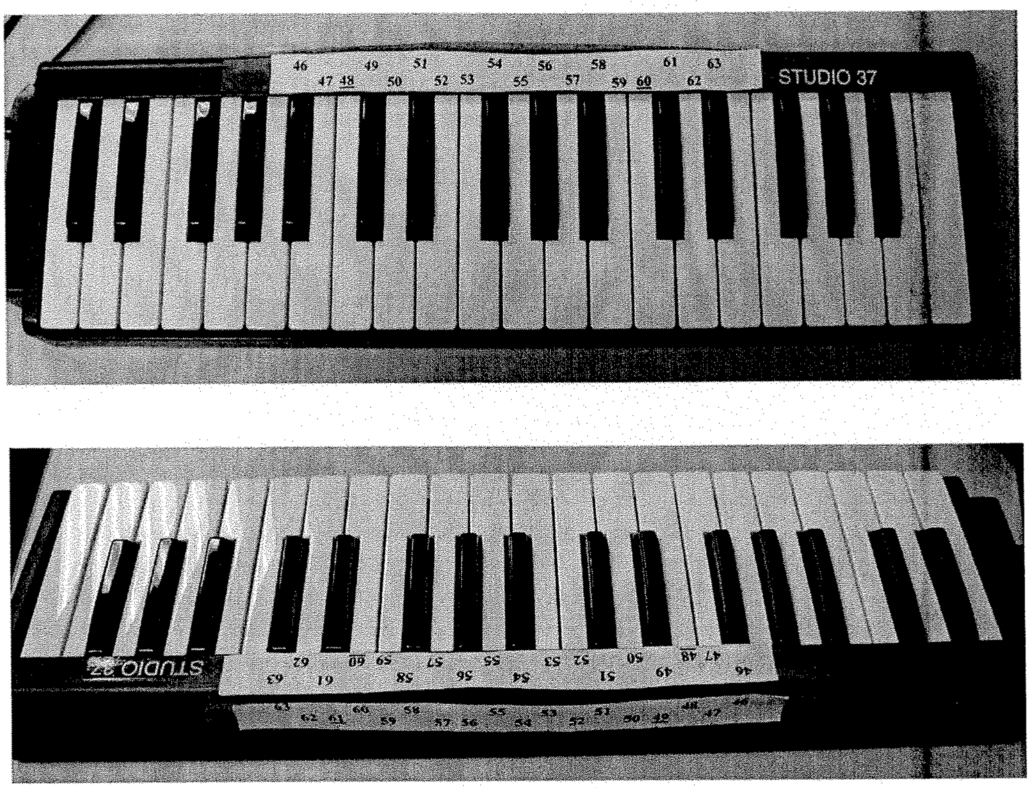

Figure 2. *The piano keyboard in its normal (top) and reversed (bottom) orientations, as seen by the participant.*

placed on either side of the computer below the monitor.

Procedure

Participants sat at a small table with the piano keyboard (MIDI controller) in front of them. The computer monitor, the loudspeakers, and the computer keyboard were located to the right of the piano keyboard. In the active condition, participants were alone and carried out the task as in Experiment 1, except that the experimenter came in and rotated the piano keyboard by 180 degrees after the first 6 blocks. When the piano keyboard was reversed, participants had to reach over its back to press the prompted keys with the index finger. This task was only slightly more awkward than pressing keys in the normal keyboard orientation and could be carried out without difficulty (see Figure 2).

In the passive condition, the experimenter (author B.H.R.) sat on the other side of the table facing the participant and pressed the piano keys with his right index finger while the participant looked on and only gave the responses on the computer keyboard. The computer monitor showing the numeric prompts was turned to face the experimenter. After six blocks of trials, the piano keyboard was rotated. The experimenter frequently checked to make sure that the participant was watching his movements.

Results

The mean ADEs in the four experimental conditions are shown in Figure 3. The effects in both conditions with normal keyboard orientation were significantly greater than zero, $t(11) = 3.96$ and 3.66, respectively, both $ps < .005$, whereas those in the reversed

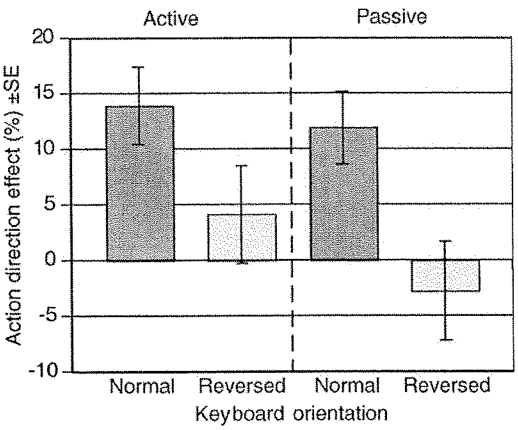

Figure 3. *Mean action direction effects in the four conditions of Experiment 2, with standard error bars.*

keyboard conditions did not differ significantly from zero, $t(11) = 0.96$ and -0.63, respectively.

A 2 × 2 repeated measures ANOVA yielded only a significant main effect of keyboard orientation, $F(1, 11) = 6.51$, $p = .03$. The main effect of action condition (active vs. passive) was not significant, $F(1, 11) = 2.12$, $p = .17$, nor was the interaction, $F(1, 11) = 0.73$, $p = .41$. The mean ADE in the baseline condition (active participant, normal keyboard orientation) was similar to the mean effect obtained for pianists in Experiment 1, only slightly smaller. As can be seen from the standard error bars in Figure 3, there were large individual differences in all conditions. Nevertheless, in the normal keyboard orientation condition most individual pianists showed the expected ADE. In the reversed keyboard condition there was no clear pattern. Some pianists showed large ADEs, suggesting that they ignored the keyboard reversal. (The ADE was defined relative to the participant's hand movement.) Some showed negative ADEs, and others hardly deviated from zero.

Discussion

Experiment 2 replicated the basic ADE in pianists. In addition, a mean effect of similar magnitude occurred when the pianists passively observed the experimenter pressing the piano keys. This finding is consistent with the close relationship between action execution and action observation that has been found in other situations and in many recent studies of brain function (Jeannerod, 2006; Rizzolatti & Craighero, 2004). Observing another person pressing piano keys in a certain order seems to trigger the same predictive mechanisms that affect pianists' perception when they press the keys themselves (Hamilton et al., 2004; Wilson & Knoblich, 2005).

When the piano keyboard was reversed, there was no significant ADE induced by either active key pressing or passive observation of the experimenter's key pressing. This result is consistent with the hypothesis that the effect is generated through an internal model that is based on past experience with particular actions using a particular instrument in a particular orientation (Imamizu et al., 2000; cf. Wilson & Knoblich, 2005). According to this view, the internal model cannot be applied when the instrument is in an unfamiliar orientation, and the ADE consequently vanishes.

From this perspective, however, it is difficult to explain pianists' substantial ADE in the computer keyboard condition of Experiment 1. Although a computer keyboard is a familiar tool for typing, it does not afford pianistic actions such as playing a scale or melody, and key presses on it are not a priori associated with tones differing in pitch. Therefore, it should not have engaged the pianists' internal model of piano playing as readily as it apparently did. A reversed piano keyboard, like a computer keyboard, does not afford realistic pianistic actions (which were not required in our experiment), but it remains a piano keyboard and thus carries with it strong associations of tones varying in pitch. Therefore, it should have engaged the pianists' internal model and should have elicited a stronger ADE than a computer keyboard did in Experiment 1.

Therefore, an alternative explanation might be considered: that two conflicting processes were present that, on average, cancelled each other. One process was the engagement of pianists' internal sensorimotor model by their hand movements on the reversed piano keyboard. This by itself would have led to an ADE similar to that obtained with a keyboard in normal orientation.

The other process was pianists' cognitive representation of the directionally reversed pitch mapping of the reversed keyboard (pitch increasing from right to left), which amounts to a reversal of the internal model's predictions. Such a strategy, if maintained consistently, would have led to a reversed ADE. Individual participants may have varied in the strength and consistency of such reversed expectations, and this may account both for the large individual differences and for the absence of a mean ADE in the reversed keyboard condition.

GENERAL DISCUSSION

Together, the two experiments demonstrate that the particular sensorimotor mappings that pianists acquire while learning to play the instrument can influence their judgements of pitch, a fundamental auditory attribute. The first experiment showed that the direction of hand movements between two consecutive key presses affects pianists' relative pitch judgements for octave-ambiguous tritone pairs to a much larger extent than it affects nonpianists' judgements. This group difference was statistically independent of the type of keyboard used (piano or computer), although pianists did tend to show a larger ADE on the piano keyboard, which was associated more strongly with their specific sensorimotor experiences as pianists.

The second experiment replicated the ADE in the active/normal piano keyboard condition and furthermore demonstrated that observing another person pressing the keys influenced pianists' pitch judgements in the same way as when they pressed the keys themselves. This finding is in line with a host of recent studies demonstrating an extensive functional overlap between systems for action execution and action perception (Jeannerod, 2006; Rizzolatti & Craighero, 2004; Schütz-Bosbach & Prinz, 2007). When the piano keyboard was reversed, however, movement direction did not influence pianists' pitch judgements systematically, neither in an active condition nor in a passive observation condition.

One plausible explanation of the ADE observed in the present experiments is that pianists have acquired particular internal forward models (Jordan & Rumelhart, 1992; Kawato, 1999; Miall & Wolpert, 1996; Wolpert & Kawato, 1998) that nonpianists do not possess. These models predict the expected sensory consequences of keyboard actions including a rise or fall in pitch depending on relative hand position on the keyboard. The predictions can shift the perception of pitch in octave-ambiguous tone pairs in the direction that corresponds to pianists' prior experience of performing action sequences on a keyboard. The tones, which have an organ-like timbre, are plausible products of playing a keyboard instrument and thus engage the pianists' internal models (cf. Drost et al., 2007).

The internal model predictions are constrained by contextual factors such as keyboard appearance, feel, and orientation. The more such factors deviate from the prototypical situation of playing piano the less the pianists' internal model will be engaged. This probably explains their smaller ADE in the computer keyboard condition of Experiment 1. Nevertheless, a computer keyboard controlling sounds was evidently sufficiently similar to a piano to engage pianists' internal models to a considerable extent. In the reversed keyboard condition of Experiment 2, however, pianists probably modified or counteracted the predictions of their internal model with a cognitive strategy of expectation reversal, with more or less success, resulting in absence of a mean ADE. This tentative explanation calls for further research that isolates the influences of internal models, cognitive strategies, and perhaps interpersonal processes such as taking the observed model's perspective on the observed effects.

The results of Experiment 2 are consistent with the idea that internal models are not only applied in action execution but also in action observation. When a pianist observes another person pressing piano keys, the perceived events are matched to one's own action repertoire on a common coding level (Prinz, 1990). This, in turn, activates the same forward models that are involved in actively playing on a piano (Ramnani & Miall, 2004; Wilson & Knoblich, 2005). As a consequence the same auditory predictions are generated, and the same ADE is present when pianists observe another person pressing the piano keys.

There are possible alternative explanations of the ADE. It is highly likely that participants formed a more or less conscious expectation (auditory image) of the pitch of the second tone in a tritone pair before pressing the second key in the sequence. Repeated exposure to the tones gives listeners a sense of the relative height of each tone within the perceived pitch range of the whole set (Ragozzine, 2001; Terhardt, 1991; Terhardt, Stoll, Schermbach, & Parncutt, 1986). If the first tone is perceived as relatively low, a higher second tone can be expected, and vice versa. Also, participants know in advance which key sequence they will perform, and this knowledge may influence their expectations via conceptually mediated associations between horizontal movement direction and relative pitch height—what Lidji and colleagues (2007) call the "piano in the head". Anticipatory auditory images, in turn, may affect the perception of the octave-ambiguous tritones (cf. Pearson, Clifford, & Tong, 2008). However, this could only explain why nonpianist musicians showed a small, but significant, ADE. Such a mechanism could not explain the influence of pianists' specific sensorimotor experience on the ADE. However, the likely existence of action-independent expectations raises the question of when and how sensorimotor experience has its effect. Does it affect pianists' expectations as soon as they are formulated, long before the second key is pressed, or does it represent an independent source of subconscious expectations that is activated by the second key press? Further research will be necessary to address these questions.

A second alternative explanation to be considered is that the ADE may have occurred post hoc: Whenever participants felt uncertain about the direction of the perceived tritone interval they may have resolved the ambiguity in favour of the judgement that was consistent with their remembered direction of movement on the keyboard and their knowledge of the pitch mapping. Again, this could work as an explanation for the small ADE observed in nonpianist musicians but it cannot easily explain the large difference in the effect between pianists and nonpianists. Could sensorimotor experience have led to a stronger response bias in pianists? Again, we encounter the broader question of when and how strong action–effect associations acquired through extensive sensorimotor experience may have their influence in the course of a temporally extended perception–action task that has both prospective and retrospective components. If the influence is mediated by an internal model that is strictly tied to action and is independent of the conscious processes of prediction and decision making, then sensorimotor experience should have its effect on perception solely at the moment of the critical action, via processes that occur without awareness. Alternatively, its influence may be temporally less definite and spread out over all stages of the task, affecting predictions as well as decisions, or possibly just one of these stages. Clearly, our present findings cannot settle this complex issue. All we can say is that we have demonstrated an effect of pianists' sensorimotor experience.

To conclude, our experiments demonstrated that pianists' particular sensorimotor learning history leads to an influence of movement direction on perceptual judgement that is not present to the same extent in other experienced musicians and is probably absent in nonmusicians (Lidji et al., 2007; Repp & Knoblich, 2007; Rusconi et al., 2006).[4]

[4] The control group in Repp and Knoblich (2007), which showed no significant ADE on a piano keyboard, was composed of Rutgers undergraduates with little or no musical training, from a rather different student population. A difference between Yale nonpianist musicians and Yale nonmusicians in the ADE remains to be demonstrated. If nonmusicians were found to show a small ADE, this might be a consequence of orthogonal action–effect compatibility: Because pitch height is strongly associated with the vertical dimension, and "up" tends to be associated with "right" (see Cho & Proctor, 2005), a L–R movement might be associated with a rise in pitch. There is some evidence that associations of pitch height with the vertical dimension are stronger in musicians than in nonmusicians (Keller & Koch, 2008; but see also Keller & Koch, 2006), so the ADE in nonpianist musicians may also derive in part or wholly from orthogonal spatial associations, rather than from knowledge of piano keyboards.

This influence is seen not only when pianists actively produce tones on a keyboard but also when they observe others performing this task. The results show that effects of action on perception do not only occur in the visual domain but also in the auditory domain. The further study of how a particular motor expertise can influence related aspects of perception provides a fruitful avenue for future behavioural research on perception–action links (cf. Casile & Giese, 2006) that can be related easily to cognitive neuroscience research (cf. Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006).

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