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RESEARCH ARTICLE

Functional relationship between cognitive representations of movement directions and visuomotor adaptation performance

Heiko Lex · Matthias Weigelt · Andreas Knoblauch · Thomas Schack

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Abstract The aim of our study was to explore whether or not different types of learners in a sensorimotor task possess characteristically different cognitive representations. Participants' sensorimotor adaptation performance was measured with a pointing paradigm which used a distortion of the visual feedback in terms of a left–right reversal. The structure of cognitive representations was assessed using a newly established experimental method, the Cognitive Measurement of Represented Directions. A post hoc analysis revealed inter-individual differences in participants' adaptation performance, and three different skill levels (skilled, average, and poor adapters) have been defined. These differences in performance were correlated with the structure of participants' cognitive representations of movement directions. Analysis of these cognitive representations revealed performance advantages for participants possessing a *global* cognitive representation of movement directions (aligned to cardinal movement axes), rather than a *local* representation (aligned to each neighboring direction). Our findings are evidence that cognitive representation structures play a functional role in adaptation performance.

Keywords Sensorimotor adaptation · Cognition · Cognitive representation · Internal model

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Introduction

In daily life, humans must constantly adapt to the incongruencies between the expected and perceived effects of our goal-directed or automated actions on the environment. Such surprising incongruencies drive the establishment of new links between sensory input and motor output and allow humans to adapt to changes in environmental conditions.

Many laboratory studies have investigated adaptation processes by conducting experiments in which participants execute straight ballistic pointing movements toward targets (e.g. Georgopoulos et al. 1981, 1983), or track a moving target on a screen (e.g. Abeele and Bock 2003). The adaptation paradigm can be described as follows: After participants are familiarized with the setup, they are introduced to a distortion and their task performance is measured over a number of trials. Usually, performance errors peak immediately after distortion onset and normalize again with extended practice. This *sensorimotor adaptation* phenomenon has been studied in the context of different distortions, such as visual (Bock and Girgenrath 2006) and mechanical (Pipereit et al. 2006) distortions.

It is well accepted that sensorimotor adaptation, as signified by specific performance improvements, is initiated by two different types of processes: The first process

involves the gradual recalibration of the sensorimotor system, while the second process involves strategic control (Bock 2005). Essentially, this recalibration process brings sensory input and motor output in accordance with each other to control for the distortion. This adaptive behavior is initiated by the transformation of an internal model (Wolpert et al. 1995) or a 'spatial realignment' (Redding and Wallace 1996) and can be described as a stepwise approximation to new environmental conditions. The strategic control process is grounded in cognitive schemes and representations, which are activated to overcome, for example, the performance disruption at the beginning of trials (Redding and Wallace 1996). Therefore, visual feedback-based movement adjustments and anticipatory mechanisms control the movement's execution. These processes are active when, for instance, closed boxes are lifted without any knowledge about their weight. After the first box was carried, it is possible to anticipate the weight of the second box in a better way, and the grip force will be immediately adjusted in advance.

Functional links between sensorimotor adaptation and cognitive functions, which are potentially the basis of this link, are often discussed. For example, when performing a sensorimotor task requiring some sort of adaption, participants' adaptive performance is better when attention is distributed between the target and cursor, rather than focusing mainly on the target or spreading attention across the whole scenario (Grigorova et al. 2006). Decreased adaptive performance in sensorimotor adaptation tasks is found among the elderly and might be caused by changes to the cognitive structures involved in decision-making and basic response speed (Bock and Girgenrath 2006).

A study highlighting not only the role of cognition in sensorimotor performance but also the necessity of possessing stored mental representations comes from Ingram et al. (2000). These authors showed that a deafferent patient (i.e. a neurological disorder, where the patient has no sensory input from his neck downwards) is able to adapt toward visual distortions (e.g. immediate and gradual gain change) in a goal-directed arm movement task when a distortion (e.g. 1.5 times gain change) was applied. However, an additional cognitive task (e.g. counting task) impaired his adaptation performance severely for more than a 60 % change. In comparison, the adaptation performance gain of the control group was also impaired, but only less than 10 %. It is important to note that in order to adapt in this task, the deafferent patient had to rely predominantly on his cognitive structures, without receiving any proprioceptive feedback from his arm movements. Ingram et al. (2000) concluded that proprioception is not an absolute requirement for adaptation. Rather proprioception is only one relevant part in the ability to adapt for visuomotor distortions.

Each of these studies mentioned so far (Bock and Girgenrath 2006; Grigorova et al. 2006; Ingram et al. 2000) underlines the important role of cognition in sensorimotor adaptation. Their results support the viewpoint that the storage of information about movements and their interaction with the environment form the basis of learning processes. Still, these studies have merely speculated about the structure of cognitive representations. The present study takes a more direct attempt to measure the link between sensorimotor adaptation performance and cognitive representations.

Researchers from fields such as cognitive psychology and cognitive robotics (Maycock et al. 2010; Schack 2004; Schack and Mechsner 2006; Schack and Ritter 2009; Stöckel et al. 2011) have provided evidence for the functional role of cognitive representations in the control of human movements. According to these studies, structured cognitive representations of motor actions are based on so-called *basic action concepts* (BACs). Analogous to the well-established notion of basic concepts in the world of objects (Mervis and Rosch 1981), BACs can be viewed as the mental counterparts of functionally relevant elementary components or transitional states (body postures) of complex movements (Bläsing et al. 2009; Schack and Ritter 2009; Weigelt et al. 2011). They are based on the cognitive 'chunking' of body postures and movement events, which possess common functions involved in the realization of action goals. Unlike object concepts, BACs do not refer to behavior-related invariance properties of objects, but rather to perception-linked invariance properties of movements.

For example, Schack and Mechsner (2006) studied the tennis serve to investigate the nature and role of long-term memory in skilled athletic performance. Using the Structural Dimensional Analysis of Mental Representations (Schack 2004, 2011), the authors analyzed high-level experts and found that the structures of their representations were organized in a distinctive tree-like hierarchy, were remarkably similar between individuals, and were well-matched with the functional and biomechanical demands of the task. In comparison, the structures of action representations in low-level players and non-players were organized less hierarchically, were more variable between persons, and were not as well-matched with the functional and biomechanical demands of the task. The results of related studies from a variety of disciplines (e.g. manual action, judo, wind surfing, dancing) have further demonstrated that cognitive representation structures in long-term memory are functionally related to performance (Bläsing 2010; Bläsing et al. 2009; Schack and Hackfort 2007; Stöckel et al. 2011; Weigelt et al. 2011).

It can be inferred from these studies that these cognitive representation structures consisting of cognitive units (such as basic action concepts in complex motor actions) are also

involved in smaller motor actions (such as pointing movements in a sensorimotor task). One functionally relevant basic cognitive unit in goal-directed pointing movements might be a representation of a movement direction.

Research in neurophysiology has provided convincing evidence for the existence of such cognitive representations of movement directions (Georgopoulos et al. 1986). Cognitive spatial-motor processes were investigated by the application of setups indicating movement directions by center-out movements toward flashed up lights. One of the earliest studies measured a significant linear increase in reaction time, when the rotation angle between a defined stimulus direction and the required movement direction increased (Georgopoulos and Massey 1987). From this finding, it was derived that performing such tasks involves a mental rotation of an imagined movement vector about its origin. Additionally, neurophysiological correlates sensitive to movement directions were found in the brains of monkeys (Georgopoulos et al. 1983). A first process in the brain indicates that directional information about visually cued arm movements (i.e. indicated by turned on peripheral lights) is encoded and can be visualized by the analysis of the neuronal population vector. A second process indicates that representations of movement directions are related to retention mechanisms in long-term memory. This is because in the absence, rather than in the presence, of a visual target, the neurophysiological signals become significantly stronger (Smyrnis et al. 1992). Caminiti et al. (1990) found that neuronal population responses are more related to movement trajectories than to end points of movements, which highlights the relevance of directions in goal-oriented pointing movements. Thus, a direction-sensitive neuronal population vector can serve as a predictor for the directions in which goal-oriented pointing movements are executed (Caminiti et al. 1991). In contrast, to findings of directional sensitive neurons in frontal areas, there is evidence that neurons in parietal lobe Brodmann area 5 are tuned positionally during movement and stationary posture. This positional tuning can be characterized by spatial coordinates defining the azimuth, elevation, and distance during reaching movements. Each of the spatial coordinates might be encoded discretely in distinct subpopulations of neurons. These neurons form classes described by a fixed tuning function. 'Initial position' neurons movement activity does not change in relation to the starting point of the movement. 'Variational' neurons are related to the difference vector between final and initial position, which is responsible for the encoding of movement direction (Lacquaniti et al. 1995). Thus, in parietal lobe area 5, movement directions are encoded in populations of neurons. Additionally, a subset of neurons found to be sensitive to preset distortion change their activity during sensorimotor adaptation. These neurons acquire directional sensitivity to the adapted direction, but this sensitivity has a limited generalization ability for all other directions (Paz and Vaadia 2009). This experimental evidence highlights the functional relevance of movement direction in goal-directed movements on a neurophysiological level.

From our point of view, sensorimotor adaptation of manual actions has to be planned and represented in terms of intended perceptual effects and future task demands. Therefore, individuals are developing structured cognitive representation of movement directions in order for the movement to be carried out and adapted successfully. Neurophysiologic evidence supports the notion that movement directions are represented in long-term memory. Therefore, it can be assumed that the sensorimotor adaptation performance in goal-directed pointing movements is fundamentally influenced by the structure of cognitive representations of movement directions.

The present study investigates individuals' cognitive representations of movement directions from long-term memory and evaluates their influence on sensorimotor adaptation performance. With this study, we attempt to examine the functional relationship between cognitive representations and sensorimotor adaptation, and the extent to which the variation in individual adaptive ability correlates with the variation in representation structures in long-term memory. From that point of view, this will be the first study to examine individual differences in adaptive ability and its underlying cognitive sources.

Methods

Data were collected from students at Bielefeld University (26 women and 19 men; mean age 23.7 years, standard deviation 4.7 years). The participants provided written consent prior to the experiments and did not receive any financial compensation. The research study was approved by the local ethics committee and conducted in accordance with the 1964 Declaration of Helsinki. All participants completed two experiments. First, they performed a standard sensorimotor adaptation task, which required center-out pointing movements to different target locations regularly distributed on a circle. Second, they judged visual and proprioceptive movement directions using the Cognitive Measurement of Represented Directions (C-MRD).

Sensorimotor adaptation task

The sensorimotor adaptation task was executed by all participants to measure their adaptive performance before and after the left–right reversal distortion of visual feedback.

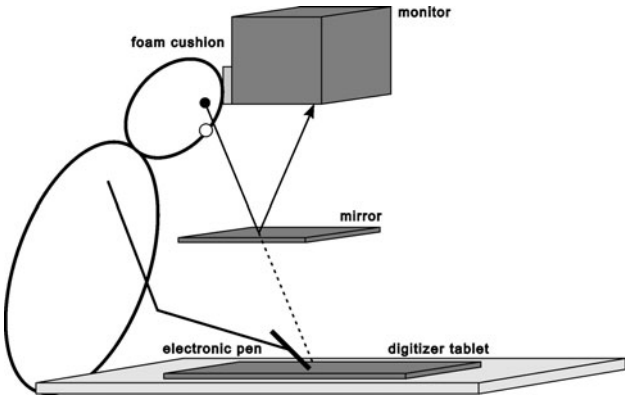

Fig. 1 Experimental setup of sensorimotor adaptation task. Participants moved an electronic pen in one of eight movement directions indicated by *yellow dots* on a *black* background. The projection of the screen was provided by a tilted mirror which occluded vision of the participant's own hand as they executed the task. *Target dots* appeared in the working plane. Participants leaned their head against a foam cushion to ensure a stable, constant position

Apparatus and task

Adaptive performance was assessed using a standard pointing experiment, in which pointing movements are executed on a digitizer tablet (Genius NewSketch 1812 HR). Participants sat in front of a 15-inch standard monitor facing downwards (see Fig. 1). To ensure a stable and constant position throughout the whole experiment, participants leaned their head against a foam cushion fixed to the monitor at a height of 130 cm. Visual real-time feedback of hand movements was provided by a red cursor cross (8 mm in length and width) displayed on the screen. Vision of the screen was available indirectly, through a tilted mirror. The mirror occluded vision of the individual's own hand in order to prevent the use of visual control strategies on the hand movements. Screen-to-mirror and mirror-to-digitizer tablet distance was adjusted to 21.5 cm each. Hence, all projected images of target dots, center location, and the red cursor cross appeared in the same plane of working space. A height-adjustable chair assured a comfortable position and permanent visibility of the complete screen.

The participants' task was to execute straight and ballistic (i.e. open loop) center-out movements toward one of eight randomly appearing, equidistant, peripheral target locations as accurately as possible. Similar to previous studies which used this standard sensorimotor adaptation task (cf. Bock 2005; Bock and Girgenrath 2006; Miall et al. 2004), the center location always served as the start position for the next movement. The target locations were yellow dots sized 8 mm in diameter, displayed on a black background in an arc radius of 10 cm. Target dots stayed on the screen until they were reached by the cursor cross or for a maximum of 700 ms. If participants failed to reach the target location, a new target automatically appeared on the screen after 5 s. Within each 30 s trial, as many pointing movements as possible were executed. The inter-trial interval was set to 5 s.

The experiment started with three practice trials, to familiarize participants with the setup. Afterward, baseline data were collected for five undistorted trials with normal vision in Baseline 1 (BL1), followed by five undistorted trials without vision of the red cursor cross in Baseline 2 (BL2).

During BL2 trials, participants were forced to execute the pointing movements more intuitively, because the red cursor cross disappeared when participants moved more than 10 mm away from the center position, and appeared again when they re-entered this area. Participants still needed the cursor cross to find their way back to the center position and move on to the next movement target. During the adaptation phase (AP), the (normal) visual feedback relationship between sensory input and motor output was distorted by a left–right reversal mirrored along the sagittal axis (i.e. 180° rotation). For example, in this condition, participants would need to execute a pointing movement toward the upper right corner if they wanted to reach the upper left corner. Full visual feedback of the cursor cross was provided in the adaptation phase, which consisted of a total of 30 trials. After a five minute break, five distorted trials without full visual feedback were performed in the phase of persistence (PP) to test for the persistence of adaptive behavior over time.

Data analysis

To quantify participants' pointing performance, the initial angular error (IAE) was measured for each pointing movement. The IAE was defined as the difference between the straight target direction and the initial hand movement direction. Thereby, the straight target direction was defined as the direct line between the hand position at movement onset (the start position) and the target location. The initial hand movement direction was defined as the line between the hand position at movement onset and the location of the hand when the first peak velocity was reached. To exclude small corrective adjustments, the critical minimal cursor velocity was set to 30 mm/s. This error detection mechanism was used because it is largely unaffected by the visual feedback-based corrective modifications which occur during the later phases of a single pointing movement. The IAE was averaged over all executed pointing movements and then aggregated into phases. To compare phases of identical length, each phase consisted of the average IAE of five consecutive trials. An analysis of variance (ANOVA) with repeated measures was conducted to verify differences between the adaptation phases.

Cognitive representation of movement directions

For use in this study, the C-MRD was developed to be specifically applicable to the assessment of the cognitive representations of movement directions. The applied sensorimotor task consisted of pointing movements in distinct directions. Thus, movement directions are the physically relevant features for the sensorimotor adaptation task. The C-MRD method investigates the cognitive representations of movement directions as relevant features. Participants experienced all movement directions (i.e. cognitive units) used in this method both visually and proprioceptively. The reason that the movement directions have to be experienced by the described input modalities was given by van Beers et al. (2002). They showed evidence that sensorimotor adaptation performance relies on the contribution of proprioceptive feedback as well as on the contribution of visual feedback when adapting toward a visual distortion in terms of sagittal displacement (van Beers et al. 2002). The present study is planned to learn about the relationship between adaptation behavior and cognitive representations. Thus, the measurement of cognitive representations of movement directions must integrate proprioceptive features as well as the visual feedback of executed movement directions as two integral components of the cognitive representations. For this reason, both input modalities were integrated in the measurement of the cognitive representations of movement directions. Consequently, the conditions of the sensorimotor adaptation task and the C-MRD task were matched as much as possible.

Apparatus and task

Participants sat in front of an apparatus, which sat on a table (see Fig. 2). Participants' cognitive representation of movement directions was assessed using a splitting procedure, that is, a comparison of each movement direction with every other direction, but not with itself. In this splitting procedure, participants were asked to grasp a wooden stick in the center position of the apparatus and move it once to the lit up target direction. The twelve target directions were distributed at equidistant intervals around a circle. For each direction, there was a slot in the wooden platform to guide the wooden stick outward from the center. As soon as stick reached the end of the slot, the movement was redirected to the center position. There was a brief rest break before the next target direction was lit up by the experimenter. After two consecutively executed movements into different slots, participants were asked to judge on the basis of their own subjective criterion whether the two executed movement directions appeared similar to them, or different. They did not state verbally whether the two executed movement directions are the same, or

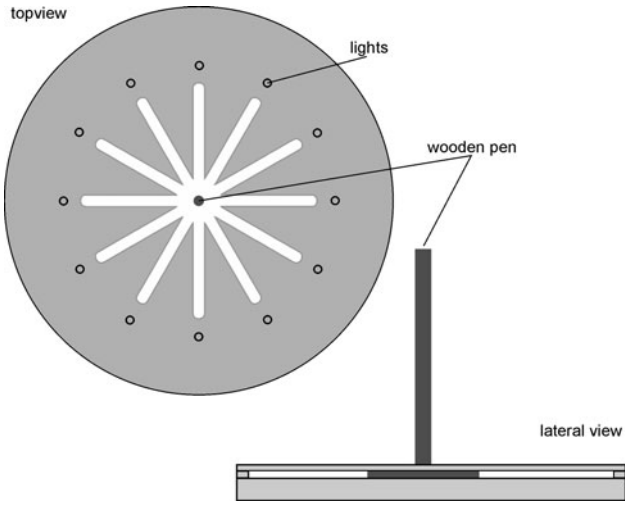

Fig. 2 Experimental setup to measure the cognitive representation of movement directions. The apparatus consisted of twelve movement directions indicated by 12 slots in a wooden plate. All movement directions were spread equally around a *circle*, starting with the first slot in the straight upward position and another slot at each 30° rotation. Participants received visual and proprioceptive feedback from their movements as they moved a wooden pen in the direction of a lit up target. After two executed movements, participants made subjective judgments about similarity

different. Furthermore, decisions were allocated to a positive (i.e. if movement directions were judged as similar) or a negative (i.e. if movement directions were judged as dissimilar) subset and logged on a standard personal computer by the experimenter immediately after participants' answered verbally. Decisions were made without any time limits. One randomly chosen movement direction remained in the reference position (first of the two movements performed) until it was compared with every other movement direction (second movement performed). Once all decisions for the reference direction were completed, another movement direction became the reference position. This process lasted until all possible combinations of movement directions had been compared. The splitting procedure revealed insight into the general formation of cognitive units (i.e. movement directions).

Data analysis

The data analysis of participants' decisions consisted of three steps. First, for each reference direction, the described splitting procedure created a positive and a negative subset of movement directions. Movement directions in each subset were assigned a score reflecting their similarity to the reference direction. The score was based on the number of elements in the subset and the sign of the subset (positive/negative). This procedure resulted in a score vector for each reference direction. The score vectors of all reference

directions were concatenated into a score matrix. Each row of the score matrix corresponded to one reference direction. Rows were transformed by a z-normalization and, thus, converted to a relative position of each reference direction in a multidimensional direction space. This normalized position matrix was then used to calculate the Euclidian distances between all reference directions, resulting in a distance matrix.

Second, the representations of movement directions were calculated using an unweighted average-linkage hierarchical cluster analysis applied to the Euclidian distances matrix. The distance between a given pair of directions is reflected by the numbers at the conjunctions within each dendrogram (i.e. cluster structure). The smaller the Euclidian distance between two directions, the more similarly the two directions were subjectively perceived, and the closer they are represented together in human long-term memory. The critical Euclidian distance is statistically estimated as the value $d_{crit} = 4.552$ for a significant alpha-level of $p = .01$. All connected structures below the critical value form distinct clusters. Conversely, all movement directions with a Euclidian distance above the critical value are not integrated into distinct clusters.

Third, the generated representations of movement directions were tested for structural homogeneity using a within- and between-groups invariance measure. In the present analysis, the statistical threshold for accepting invariance between two structures is set to $\lambda = .68$ (Schack 2004).

Representation of movement directions by adaptive performance level

Finally, participants' cognitive representations of movement directions were assessed with regard to their sensorimotor adaptation performance. This analysis connected the results of the sensorimotor adaptation task with participants' cognitive representation structures.

Therefore, individual sensorimotor adaptation performance was quantified by an adaptation index (Ak, Bock and Girgenrath 2006). This index (A_k) compares the IAE at distortion onset (AP_1), subtracted by the error in the last adaptation phase (AP_6), in relation to the error at distortion onset (AP_1), subtracted by baseline error (BL_1). The adaptation index is calculated as

$$A_k = \frac{AP_1 - AP_6}{AP_1 - BL_1}$$

where k is the participant's indicator. An A_k of 1.0 indicates perfect adaptation back to the baseline performance level, whereas an A_k of zero indicates no adaptation at all, that is, no performance improvement compared with baseline level. The adaptation index is used as a criterion to quantify participant's adaptation performance by a semi-quantitative analysis (Abeele and Bock 2003; Bock and Girgenrath 2006). After the calculation of the adaptation index for each participant, they were sorted according to their adaptation index and ranked in a descending order. The whole list of participants was then split into three equal thirds. The top third of participants were classified as *skilled adapters*, the middle-third as *average adapters*, and the lower-third as *poor adapters*. Depending on the individual adaptation performance indicated by the adaptation index within each sub-group (i.e. skilled, average, and poor adapters), the cognitive representations were analyzed by calculating the mean cluster solutions for the three categories of adapters.

The resulting subgroup dendrograms were tested for structural homogeneity (i.e. invariance measure between evolved cluster solutions) to verify skill-related differences based on the cognitive representation structure.

Results

Figure 3a illustrates the time course of the IAE in the sensorimotor adaptation experiment for each group. For all participants, the results of the ANOVA with repeated measures showed a main effect for the factor *phase*, $F(3.4, 147.6) = 30.358$, $p < .001$. Mauchly's test revealed that the sphericity assumption was violated, $\chi^2(14) = 53.379$, $p < .01$. Therefore, the degrees of freedom were corrected by estimation of sphericity according to Greenhouse–Geisser ($\varepsilon = .671$). A simple contrast analysis of all adaptation phases revealed successful adaptation during all phases in contrast to the first phase ($p < .001$). A non-significant difference between adaptation phase six and the phase of persistence, $t(44) = .850$, $p = .40$ (2-tailed), indicated that participants' adaptation behavior persisted over time.

The adaptation index quantified participants' adaptation performance in comparison with the undistorted baseline condition. Participants adapted to 61 % toward the distortion of the visual feedback in terms of a left–right reversal, indicated by $A_k = 0.61$ (SD = 0.28). Figure 3b shows the results of the third split, after sorting participants in a descending order according to their adaptation index, starting with the best adapters. In contrast to average ($A_k = 0.66$; SD = 0.08) and poor adapters ($A_k = 0.28$; SD = 0.14), skilled adapters ($A_k = 0.90$; SD = 0.06) nearly reached their baseline performance again.

To link the groups formed by the adaptation index to the cognitive representation structures, the mean cluster solutions of the cognitive representations were calculated in the last analytic step. Figure 4 illustrates the dendrograms (i.e. cluster structures) which resulted from the cluster analysis,

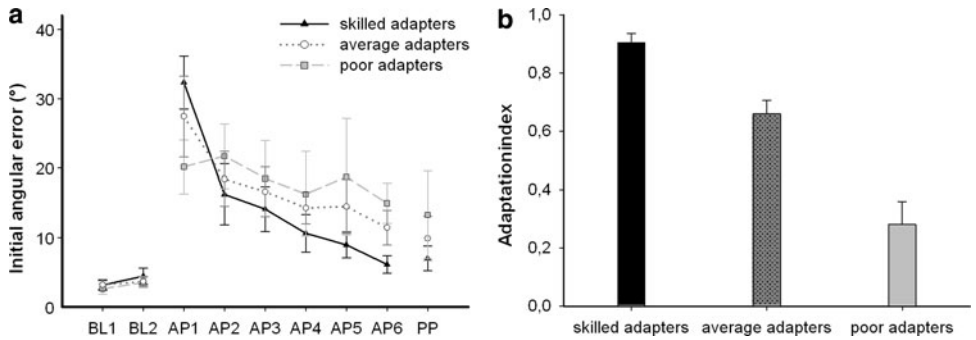

Fig. 3 **a** Adaptive behavior toward a distortion of visual feedback, including undistorted baseline conditions. The data points show the mean IAE (the difference between initial hand direction and target direction) as a function of trials in the study for each group. Five consecutive trials are aggregated into each phase. The phases represent the baseline (BL) phases one and two, the adaptation phases (AP) one to six, and the phase of persistence (PP). The *error bars* represent a 95 % confidence interval. **b** Adaptation index of visuomotor adaptation task. *Vertical bars* show mean adaptation index of the skilled (SA), average (AA), and poor adapters (PA). *Error bars* represent a 95 % confidence interval. Adaptation index of $A_k = 1.0$ represents adaptation performance back on baseline level. Adaptation index of $A_k = 0.0$ represents no adaptation toward the visual distortion

including an illustration of the cluster structures depicted as directional arrows. The cluster structures display the mean cognitive representation structure of movement directions for each adaptation group. The dashed gray horizontal line indicates the critical value $d_{crit} = 4.552$ for a significant alpha-level of $p = .01$. The numbers at the bottom indicate the movement directions, starting with *one* in the straight upward position and continuing at each 30° interval.

The mean representation structure of the *skilled adapters* group consists of three clusters. Not all movement directions are integrated in the evolved cluster structures. It is also interesting that one cluster consists exclusively of two cardinal movement directions (10 and 4), indicating the importance of these directions in the cognitive representation structure. The representation of movement directions for this group is strongly aligned to the cardinal axes (i.e. the sagittal and horizontal axis). Average adapters' mean representation structure shows the integration of all movement directions and the formation of four cluster structures. The resulting dendrograms integrate movement directions along the cardinal axes, but not as prominently as is seen in the *skilled adapters* group. The mean cognitive representation structure for *poor adapters* forms six clusters integrating two movement directions each. Thereby, every two neighboring movement directions form a coherent cluster structure. The movement directions in the cardinal axes did not show a greater prominence than other movement directions for this group, in contrast to the other two groups.

The evolved cluster structures were tested for structural homogeneity (i.e. invariance) between all three groups. The suggested statistical threshold for accepting invariance between different cluster solutions is defined as $\lambda = .68$. The comparison between cluster solutions of all groups with each other showed no invariance between groups; $\lambda_{SA \text{ to } AA} = .41$, $\lambda_{AA \text{ to } PA} = .37$, and $\lambda_{SA \text{ to } PA} = .30$. Skilled adapters' *global representation of movement directions* (aligned to cardinal axes) is advantageous compared with poor adapters' *local representations of movement directions* (not aligned to cardinal axes, but rather aligned to neighboring directions) with regard to the sensorimotor adaptation task. Having a global representation of movement directions is advantageous in the herein applied sensorimotor adaptation task because of the functional relation to the used visual distortion.

Discussion

The results of these experiments present evidence for a link between cognitive representations of movement directions and sensorimotor adaptation performance. It was found that having a *global cognitive representation of movement directions* aligned to the cardinal movement axes in the sagittal and horizontal planes is beneficial in an adaptation task which has a mirroring of visual feedback along the sagittal axis. On the contrary, having a *local cognitive representation of movement directions* diminishes adaption performance in the same sensorimotor task.

These experiments enable us to give the first insights into how movement directions are stored in human long-term memory on a cognitive level. This information allows us to expand already existing findings about the memory-related neurophysiologic mechanisms, which underlie the execution of goal-directed pointing movements in distinct movement directions (cf. Georgopoulos et al. 1986; Wu and Hatsopoulos 2006, 2007).

Interestingly, the present results relate well to findings from neuropsychological research on patients. In an early study, Bálint (1909) investigated a patient with a bilateral

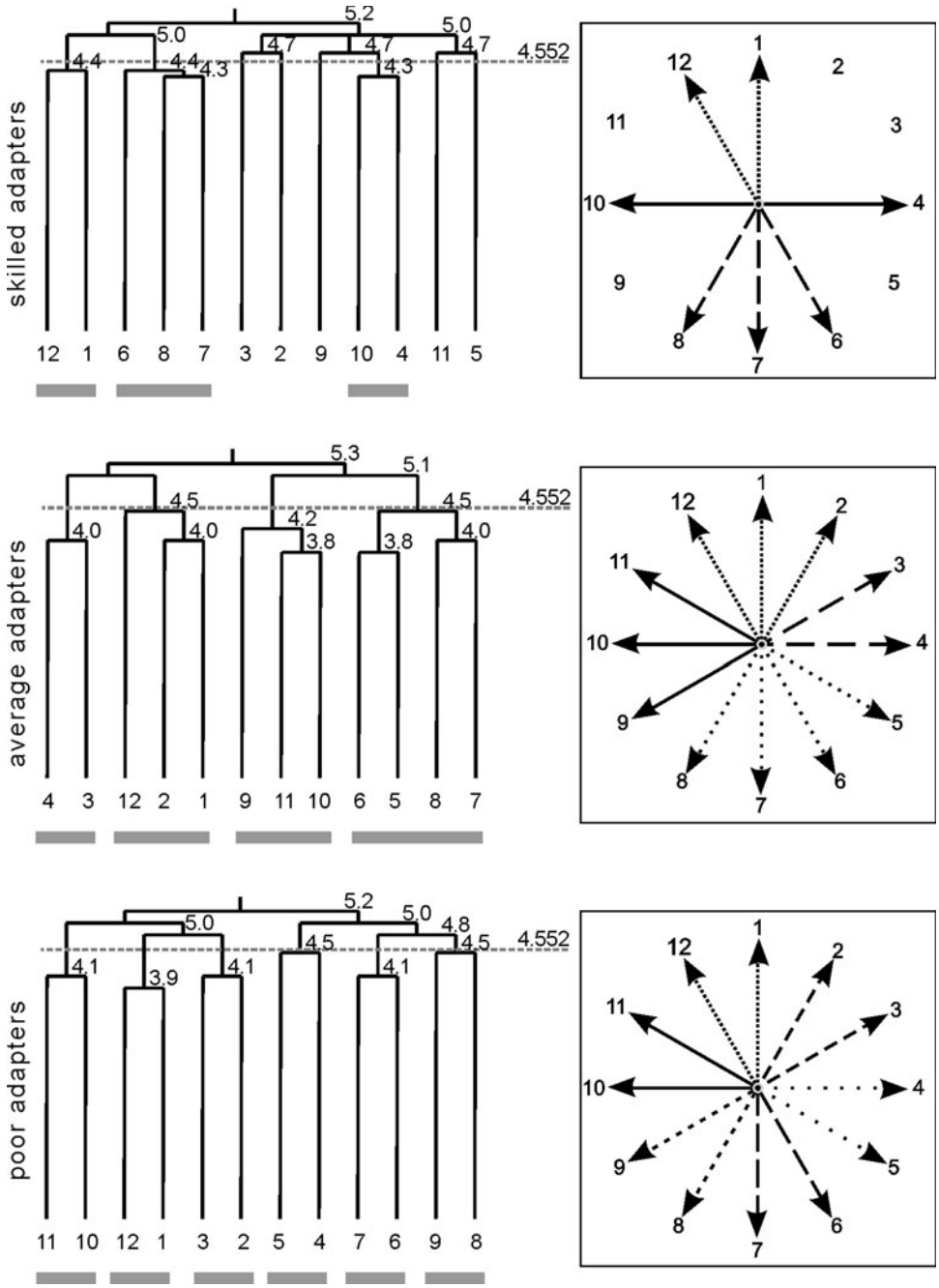

Fig. 4 Cognitive representation of movement directions. *Dendrograms* (*left*) show the results of the three groups. The *numbers* at the *bottom* show the movement directions continuously increasing every 30° starting with 1 in the straight upward position. To reflect remoteness between a given pair of directions, the numbers at the conjunctions indicate corresponding Euclidian distances. The resulting cluster structures (indicated by *solid gray bars* at the *bottom*) are revealed by a critical value $d_{crit} = 4.552$ for a significant alpha-level of $p = .01$ marked by the *horizontal gray dashed line*. On the right-hand side of each dendrogram the identical cluster solution is illustrated by *directional arrows* pointing into the corresponding movement directions. *Arrows* depicted in identical manner (*dashed*, *dotted*, or *solid*) represent the clusters in the dendrograms

parietal lesion having difficulties in executing accurate reaching movements. Usually, parietal patients are unable to match information about target location, eye and hand position, and movement direction. Moreover, neurons in the superior parietal lobe can be regarded as directionally sensitive (Battaglia-Mayer and Caminiti 2002). Within parietal patients, it can be distinguished, for instance, between two different cognitive-motor disorders: optic ataxia and directional hypokinesia. Optic ataxia is characterized by a disordered composition and control of directional hand movements (i.e. end-point errors of hand movements) in the absence of visual feedback (Caminiti et al. 2010). But, proprioceptive and tactile information can help to execute directional hand movements more accurately (Kolb and Whishaw 1996). Directional hypokinesia is characterized as an impaired representation of action space. This lesion prohibits normal movement execution toward targets in the contralesional part of egocentric space. This is preferentially described by a prolonged reaction and movement time (Caminiti et al. 2010). This means that patients with optic ataxia performing with impaired components (e.g. general motor programs) are responsible for motor execution. The representation of space is not impaired, because other movement feature dimensions

(i.e. proprioceptive or tactile movement feedback) can help to reach the target appropriately (Kolb and Whishaw 1996). People with directional hypokinesia possess an exact movement execution, but they refer to impaired, respectively, wrong space representations. Finally, the reaching disorder in optic ataxia does not show the strict directional polarity (i.e. or hemispherical effects), as has been described for directional hypokinesia (Battaglia-Mayer et al. 2005). The experiment found advanced adaptation behavior for participants who possess a cognitive representation of movement directions functionally related to the visual distortion in the adaptation task. Thus, it could be speculated that people with optic ataxia possess functionally organized representations of movement directions, whereas people with directional hypokinesia do not possess such representation structures. Although, at the moment, this is mere speculation about the cognitive representation of movement directions in these patients and more research on this topic is necessary. In the future, it therefore seems interesting to investigate patients with these disorders in order to learn more about their representations of movement directions. Another interpretation could lead to a speculation about the application of functional reference axes. It is possible that patients with such disorders (i.e. directional hypokinesia or optic ataxia) posses different abilities in the recognition of inconsistencies between a reference axis and afforded movement directions.

Previous work on sensorimotor adaptation mechanisms has demonstrated that it is necessary to implicitly compute a directional error by recognizing inconsistency between a reference axis in the applied coordinate system and the actual movement direction in pointing. A successful adaptation will then be achieved by a reduction of the directional error through a realignment of the reference axis. Thus, the behavior will be adjusted progressively (Krakauer et al. 2000). For example, the diametrical cluster (i.e. direction 4 and 10) might form a kind of reference axis within skilled adapters' cognitive representation of movement directions connecting left- and the right-ward directions or left and right hemispheres, which makes it easier to adapt to a distortion in terms of a left–right reversal. The results of the experiments presented here demonstrate that matching the demands required in the adaptation task (i.e. mirroring along the sagittal axis) and the functionally related cognitive representations of movement directions (i.e. a global representation which is aligned to cardinal axes) is advantageous to adaptation performance.

Moreover, past research has shown that interference between different sensory distortions in adaptation tasks (i.e. force field and visuomotor rotation adaptation) led to observable performance errors if they address the same kinematic parameter (Tong et al. 2002). These errors may be due to a representation of both distortions in one unique coordinate system. Our findings support the theory that a task-dependent cognitive representation can be accessed from memory, and therefore, a direction-sensitive cognitive representation will be applied in directional tasks. Thus, the structure of cognitive representations determines the performance level in sensorimotor adaptation tasks with similar kinematic distortions. If two different kinematic parameters want to access the identical cognitive representation structure (i.e. the representation of movement directions) to execute goal-directed movements in distinct directions, they will compete for the identical resource, which will lead to a decrease in actual performance.

It can be assumed from our findings that movement directions are represented in human memory in a distinct and individual manner, but the way the cognitive representation structure is applied under diverse conditions might vary. The cognitive representation of movement directions will be developed, activated, and applied in accordance with the executed motor task. Aside from the relevance of the accordance between the executed motor task and the relevant cognitive representation, it might be a chunking mechanism underlying the performance advantages in skilled adapters. Experiments investigating the learning of movement sequences (e.g. Panzer et al. 2006; Braden et al. 2008) showed that there is a decrease in response time when a movement sequence is reproduced. A reduction in response time found in trained experts (intervention group) is explained by the decreased duration of some, but not all elements being produced in the movement sequence. Thus, two or more elements of the movement sequence are chunked and allow the motor system to respond faster, because they are treated as relatively independent subsequences. A similar mechanism is detected in the current study. Expert performance in sensorimotor adaptation might rely on advantages achieved by a chunking of cardinal movement directions in the cognitive representation structure. These chunks allow a faster (i.e. in fewer trials) adaptation toward a distortion which is functionally similar according to their representation structure than is seen in a person whose structure does not classify the distortion as similar. For this reason, it may be easier for skilled adapters to develop necessary and adequate motor commands and achieve results which are more similar to undistorted trials.

A global cognitive representation of movement directions appears to be advantageous to performance in the utilized adaptation task, whereas a local cognitive representation leads to a disadvantage in the same task. Theoretically, it can be hypothesized from our findings that having a local representation of movement directions (i.e. the clustering of neighboring movement directions without the prominent role of cardinal axes) may be beneficial in a sensorimotor adaptation task in which visual feedback is

only rotated a few degrees (e.g. 30° clockwise or counter-clockwise rotation). Still, further research is necessary to test this assumption, because it is also conceivable that a global representation of movement directions (i.e. clustering around the cardinal axes) generally facilitates sensorimotor adaptation and may still be more beneficial than a local representation, even under the aforementioned conditions.

The approach used in this study overcomes the traditional perspective of studying cognition and action separately. Our approach integrates the measurement of cognitive representations of movement directions in the research of sensorimotor control performance and helps to understand the involved cognitive mechanisms as suggested by Georgopoulos (2000). It can be summarized that the structure of cognitive representations concerning movement directions (the individualized cognitive categorization of movement directions) plays a critical role in sensorimotor adaptation tasks. This supports not only the argument that learning is mostly related to the development and change of cognitive structures in memory but, furthermore, that motor performance is based on an interaction between sensorimotor and cognitive systems (Schack and Ritter 2009).

In summary, the present findings confirm the notion that sensorimotor adaptation performance is influenced by the structure of cognitive representations of movement directions, as a strategic control mechanism (see Redding and Wallace 1996). If a global cognitive representation of movement directions is functionally related to the demands of a sensorimotor adaptation task (i.e. visuomotor distortion in terms of a mirroring along the sagittal axis), the adaptation performance will be facilitated. It is concluded that the structure of cognitive representations of movement directions can be seen as an indicator and a predictor for adaptation performance.

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