Enhanced visuomotor learning and generalization in expert surgeons

AUTHORS: REDACTED AFFILIATIONS: REDACTED

Although human motor learning has been intensively studied for many decades, it remains unknown whether group differences are present in expert cohorts that must routinely cope with and learn new visuomotor mappings such as expert minimally invasive surgeons. We found that expert surgeons compensate for a visuomotor perturbation more rapidly and to a greater extent than naive controls. Modelling indicates that these differences in expert behavioural performance reflects greater trial-to-trial retention, as opposed to greater trial-to-trial learning rate. We also found that surgeons generalize to novel reach directions more broadly than controls, a result which was subsequently verified by our modelling. In general, our findings show that minimally invasive surgeons exhibit enhanced visuomotor learning and spatial generalization.

Keywords: Visuomotor adaptation; sensorimotor learning; generalization; experts; surgery; minimally invasive surgery

Introduction

Human motor learning has been intensively studied for many decades [1], [2]. However, it remains unknown whether group differences are present in expert cohorts that must routinely cope with and learn new visuomotor mappings such as minimally invasive surgeons.

Laparoscopic or minimally invasive surgery (MIS) is rapidly replacing traditional open surgery for many procedures due to its major benefits for patients over conventional open surgery including reductions in infection risks, recovery times, scarring, and overall hospital stays [3]. Despite these advantages, the task environment in MIS places high demands on surgeons, increasing the difficulty relative to open surgery for both initial learning [4] and ongoing performance [3], [5], [6]. Since laparoscopic instruments are controlled through small insertion points in the skin, instrument movements are often mirror-reversed and counter-intuitive (e.g., leftward hand motion produces rightward instrument tip motion, and vice versa). Because surgeons receive visual feedback indirectly via a laparoscopic camera that is in turn projected to a video display, rather than through direct observation, they must also contend with a range of visualization problems including absent depth information, variable magnification, and a restricted and frequently distorted (e.g., rotated) field of view. These factors, which are often subsumed under the general rubric of "challenges for hand-eye coordination" [7], also impose heavy computational demands on the brain and likely contribute to the significant increase in time to achieve proficiency in MIS compared to open surgery [8], [9].

A related and potentially deeper explanation for why MIS is difficult to learn is that it requires complex sensorimotor transformations [10], [11] - that is, the conversion of sensory inputs into appropriate motor commands [12]. These transformations are not trivial, and are known to introduce errors even for simple goaldirected movements such as pointing to a visible target [13], [14]. Moreover, because this sensory-to-motor mapping can and often does change during MIS such as when the laparoscopic camera rotates relative to the workspace or the fulcrum point of the instrument shifts, the same motor commands will not always lead to the same outcome. Consequently, surgeons must be particularly adept at learning new visuomotor transformations so they can maintain accurate and consistent motor performance during a procedure despite these fluctuations. To appreciate the inherent challenges involved, one can imagine trying to use a computer mouse if the mapping between mouse and cursor movement frequently and unpredictably changed.

If MIS introduces challenges for learning appropriate visuomotor transformations, this suggests that expert surgeons, who have successfully overcome these challenges, might perform better than naive controls in a standard visuomotor adaptation task in which a novel mapping is imposed between hand motion and the corresponding visual feedback [15], [16]. This is either because (1) they will have spent much more time practicing compensating for visuomotor perturbations, (2) they are inherently more adept than most people at compensating for visuomotor perturbations and this is part of what makes them good surgeons in the first place, or (3) some combination of both these factors. The current literature does not address the plausibility of either of these possibilities. For instance, it is unknown to what degree the basic neural and cognitive processes that drive visuomotor adaptation are capable of enhancements in learning and performance in the first place. Moreover, it has never been directly shown that expert surgeons derive their skilled behavior from better visuomotor adaptation ability. This is precisely the hypothesis we sought to test in this study.

We predicted that expert minimally invasive surgeons would compensate more rapidly and more completely for a visuomotor perturbation and therefore experience smaller errors, and would exhibit a different pattern of generalization of their learning than naive controls in a standard visuomotor adaptation task [16,17]. Our results were generally consistent with these hypotheses.

Methods

Participants

10 expert surgeons and 10 naive controls participated in the study. All were right-hand dominant (LQ > 70) assessed using the ten-item version of the Edinburgh Handedness Inventory [17], with normal or corrected to normal vision and no reported motor impairments. All surgeons (age 47+/-14 years; 9 males, 1 female), were from [redacted for review] Hospital, and had completed greater than 100 laparoscopic procedures according self-report. In particular, in our sample of 10 MIS surgeons, they reported having completed 100, 150, 500, 900, 1000, 1000, 1000, 1500, 3500, and 22000

MIS procedures). Controls $(23 \pm 3 \text{ years}; 4 \text{ males}, 6 \text{ females})$ were [redacted for review] University undergraduates with no prior medical or surgical training and limited video game use $(\leq 3 \text{ hours per week})$ [18][19][20]. All participants gave informed consent to participate and the experimental protocols were approved by the [redacted for review] Human Research Ethics Committee. Sample size was consistent with field-standard conventions for visuomotor adaptation and generalization experiments [21],[22],[23] as well as recent studies investigating group differences in visuomotor learning [24].

Experimental Apparatus

A unimanual KINARM endpoint robot (BKIN Technologies, Kingston, Ontario, Canada) was utilized in the experiments for motion tracking and stimulus presentation (Fig 1a-c). The KINARM has a single graspable manipulandum that permits unrestricted 2D arm movement in the horizontal plane. A projection-mirror system enables presentation of visual stimuli that appear in this same plane. Subjects received visual feedback about their hand position via a cursor (solid white circle, 2.5 mm diameter) controlled in real-time by moving the manipulandum. Mirror placement and an opaque apron attached just below the subject's chin ensured that visual feedback from the real hand was not available for the duration of the experiment.

Experimental Procedure

Participants were instructed to perform fast and accurate point-to-point reaching movements with the dominant (right) arm using cursor feedback, whenever it was available. Subjects performed reaches from a start target located at the center of the workspace to 11 different target locations 9 cm away from the start target and spaced 30 deg apart (Fig 1d) The start target was a solid red circle (5 mm diameter), and each reach target was a solid green circle (5 mm diameter). The appearance of the reach target served as the go cue. Participants were positioned so that the starting target was directly in front of their torso.

The experiment began with a familiarization phase of 33 reach trials (3 per target in pseudorandom order) with veridical visual feedback provided throughout the reach. After the familiarization phase, participants

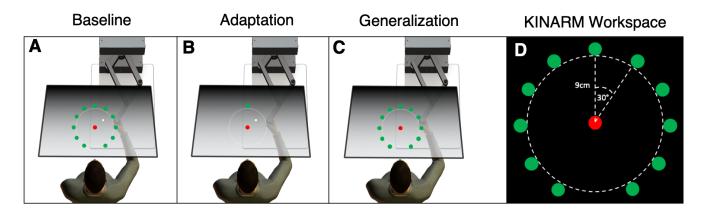


Figure 1. Experimental paradigm. (A) During the baseline phase (196 trials), participants performed reaches to 1 of 11 targets with full visual feedback for 2/3 of the trials and no visual feedback for 1/3 of the trials, (B) During the adaptation phase (110 trials), participants performed reaches to 1 target with visual feedback rotated at the endpoint of the movement, (C) During the generalization phase (66 trials), participants performed reaches to 1 of 11 targets (10 untrained target directions) without visual feedback, (D) Target array used in the experiment.

rested for 1 minute. The baseline phase consisted of 198 reach trials across all 11 target directions (18 trials per target). For 2/3 of the reaches (132 trials), veridical cursor feedback was provided throughout the trial. For the remaining 1/3 (66 trials), visual feedback was withheld. During no-feedback trials, the cursor disappeared as soon as the hand left the start target. During the return movement, cursor feedback was not provided. However, to help guide the participant's hand back to the start target a green ring centered over the start target appeared with a radius equal to the distance between the hand and start target. Once the participant's hand was 1 cm from the start target the ring was removed and cursor feedback reinstated. After the baseline phase, participants rested for 1 minute. The adaptation phase consisted of 110 reaches toward a single target positioned at 0 deg in the frontal plane (straight ahead; see figure 1). As the participant reached toward the target, cursor feedback was rotated about the start target by 30 deg (CW or CCW; counterbalanced between participants). For the cursor to move directly toward the target, hand motion would need to be directed 30 deg opposite to the direction of the cursor rotation. Visual feedback was withheld for the duration of the outward reach on all trials and was only provided when the subject's hand came within 1 cm of the start target during the return movement [23]. For 90% of the trials, visual feedback was provided at movement offset for 150 ms. These trials were used for baseline correction of adaptation data. For the remaining 10% of the trials, no visual feedback

was provided during the reach or at the endpoint. These were used to baseline correct generalization data. The generalization phase consisted of 66 reaches to 1 of 11 target directions (10 untrained directions) presented in pseudorandom order without visual feedback. No visuomotor rotation was imposed during the generalization phase.

Data Analysis and Models

Movement kinematics including hand position and velocity were recorded for all trials using BKIN's Dexterit-E experimental control and data acquisition software (BKIN Technologies). Data was recorded at 200 Hz and logged in Dexterit-E. Custom scripts for data processing were written in MATLAB (R2013a). Data analysis was performed in JASP (0.9.2) and Python (3.7.3). Model fitting was done in Python (3.7.3) using the SciPy (1.4.1) library. A combined spatial- and velocity-based criterion was used to determine movement onset, movement offset, and corresponding reach endpoints [25], [26]. Movement onset was defined as the first point in time at which the movement exceeded 5% of peak velocity after leaving the start target. Movement offset was similarly defined as the first point in time at which the movement dropped below 5% of peak velocity after a minimum reach of 9 cm from the start target in any radial direction, and reach endpoints were defined as the x and y values at movement offset. Trials that failed to satisfy the minimum reach distance of 9 cm were not included in the analysis. In total, 210 trials (5.1%) across all experimental phases were discarded from the control group and 162 trials (3.9%) were discarded in total from the expert group.

To quantify baseline motor performance, reaction time (RT; reach target onset - movement onset), total movement time (MT; movement offset - movement onset), peak velocity (PV), and hand angle (HA; hand position at movement offset) were measured on each trial during the baseline phase in which no visuomotor perturbation was imposed. To investigate adaptation and generalization performance, we focused on HA. Group differences in these performance metrics were initially compared using analysis of variance (ANOVA) and Welch t-tests (α < .05). The Holm–Bonferroni method was used to correct for multiple comparisons [27]. Adaptation and generalization data for both experts and controls were baseline corrected to remove any intrinsic biases in individual reach patterns. For adaptation data, this was done by subtracting each participant's mean hand angle measured during the trials of the baseline phase, where visual-feedback was provided an movement offset, from their mean hand angle measured during the adaptation phase. For generalization data, the procedure was exactly the same except that mean hand angle was subtracted from no-feedback baseline trials. Learning rates were initially analyzed using repeatedmeasures ANOVA and Welch t-tests. Greenhouse-Geisser corrected values for ANOVAs are reported in case sphericity was violated. The Holm-Bonferroni method was used to correct for multiple comparisons [27]. Spatial generalization of learning to new target directions was compared between experts and controls using repeated-measures ANOVAs.

To more comprehensively understand our adaptation and generalization results, we also fit our data to a standard state-space model of motor adaptation [28], [29] Many dominant theories of motor learning assume that sensorimotor adaptation involves the establishment and/or modification of internal representations (so-called internal models) that map desired motor goals into the time series of motor commands needed for execution [30]. It is thought that these internal models get updated in response to error so that errors can be reduced from one trial to the next. A simple state-space model is governed by the following equations:

$$\delta_t = x_t - r_t \tag{1}$$

$$x_t = \beta x_{t-1} - \alpha \delta_{t-1} \tag{2}$$

Here, r_t is the imposed rotation on trial t, x_t is the state of the system at time t, which corresponds to the current estimate of the rotation, and δ is the error experienced on trial t. Equation 2 describes how states are updated from trial to trial. Here, $\beta \in [0,1]$ is a free parameter that determines how much of the current state x_t is carried over from the previous state x_{t-1} . That is, the system has a tendency to decay back to its baseline value (i.e., $x_{t=0}$), and β determines the rate of this decay. Because of this, β is often referred to as the *retention rate* or, or alternatively, as the *forgetting rate* parameter. On the other hand, $\alpha \in [0,1]$ is a free parameter that determines how much of the current state changes to compensate for the last experienced error (i.e., α is the *learning rate*).

Equations 1 and 2 describe a model of how motor commands are computed to accomplish a single motor goal (e.g., reach to the training target that is directly in front of you). For such a model to generate many different motor commands to accomplish many different motor goals, it needs to be augmented with the ability to maintain separate states for each motor goal (i.e., target direction). This is accomplished as follows:

$$\boldsymbol{x}_{t} = \beta \boldsymbol{x}_{t-1} - \alpha \delta_{t-1} \boldsymbol{G} \boldsymbol{s}_{t-1} \tag{3}$$

Here, x_t is a $n \times 1$ vector of states, where n is the number of states and is equal to the number of distinct motor goals, and s_t is a $n \times 1$ indicator vector used to signal which state is active on trial t (i.e., the motor goal that was planned for):

$$\mathbf{x}_{t} = \begin{bmatrix} x_{1} \\ x_{2} \\ \vdots \\ x_{n} \end{bmatrix}, \mathbf{s}_{t} = \begin{bmatrix} i_{1} \\ i_{2} \\ \vdots \\ i_{n} \end{bmatrix}, i_{j} = \begin{cases} 1, & \text{for reach } j \\ 0, & \text{otherwise} \end{cases}$$
 (4)

The error term δ_{t-1} is computed as:

$$\delta_t = \boldsymbol{x}_t^T \boldsymbol{s}_t - r_t \tag{5}$$

where x_t^T indicates the transpose of x_t . Finally, G is a generalization function that specifies how adaptation that occurs in one state influences adaptation in the other states. Since all reaches executed in our experiments are the same length, and differ only by their angular starting position, we will express G as a function

of the angular distance between the current target direction, θ_0 , and every other target direction θ_i . Following a the literature [23]], [31], we assume that the generalization of adaptation falls of as a Gaussian with distance from the goal target, θ_0 :

$$G = e^{\frac{-(\theta_0 - \theta)^2}{2\sigma}} \tag{6}$$

where

$$\boldsymbol{\theta} = \begin{bmatrix} \theta_1 \\ \theta_2 \\ \vdots \\ \theta_n \end{bmatrix} \tag{7}$$

In many cases, simple state-space models such as those described above under-predict the rate of adaptation observed immediately following the introduction of a perturbation. In response to this, visuomotor adaptation is commonly modelled as reflecting the combined contributions from two different learning processes, one fast and one slow [32],[33], as follows:

$$\boldsymbol{x}_{f,t} = \beta_f \boldsymbol{x}_{f,t-1} - \alpha_f \delta_{t-1} \boldsymbol{G} \boldsymbol{s}_{t-1} \tag{8}$$

$$\boldsymbol{x}_{s,t} = \beta_s \boldsymbol{x}_{s,t-1} - \alpha_s \delta_{t-1} \boldsymbol{G} \boldsymbol{s}_{t-1}$$
 (9)

$$\boldsymbol{x}_t = \boldsymbol{x}_{f,t} + \boldsymbol{x}_{s,t} \tag{10}$$

$$\alpha_f > \alpha_s, \beta_f < \beta_s$$
 (11)

Here, all terms are as they were for the simple one-state model, with the subscript f and s denoting the fast and slow system, respectively. Equations 10 and 11 express the constraints on the parameter values such that learning in the fast system must be faster than learning in the slow system, and that retention in the fast system must be smaller than retention in the slow system. Put another way, this ensures that the fast system is fast and labile, while the slow system is slow and stable.

Some researchers have proposed that the slow system corresponds to a truly implicit motor process, and the fast system corresponds to a cognitive process such as an explicit aiming strategy [33]. Further, these two systems are purported to have different generalization functions [34],[35]. Further, these two systems are purported to have difference generalization functions. In line with the data suggesting this, we propose that G_s is defined as a Gaussian as previously described, but that G_f is defined as a uniform shift:

$$f(\theta) = C \tag{12}$$

where *C* is a scalar free parameter.

Our experiment includes three phases (i.e., baseline, training, and generalization), and the context of each of these phases may appear quite different to participants. For example, during baseline, reaches are made and feedback is given to all targets. During training, reaches are only made to the training target. During generalization, reaches are again made to all targets, but feedback is withheld. Because of these context differences, it is possible that only a portion of the adaptation acquired during the training phase will transfer to the generalization phase (e.g., as is the case in studies of inter-limb transfer of visuomotor adaptation, where the context shift corresponds to switching hands). To allow for this possibility we assume (where the transfer between training and generalization occurs on trial t = 306):

$$x_{f,t=306} = \gamma_f x_{f,t=306} \tag{13}$$

$$x_{s,t=306} = \gamma_s x_{s,t=306} \tag{14}$$

Where $\gamma_f \in [0, 1]$ and $\gamma_s \in [0, 1]$ are scalar free parameters.

We fit this state-space model to the trial-by-trial endpoint hand angles observed in the reported experiments, and used the parameter estimates from the best-fitting model as dependent measures. The model is fully specified by equations 8, 9, 10, and 11. The behaviour of the model is fully characterised by eight parameters: two learning rates ($\alpha_s \in [0,1]$ and $\alpha_f \in [0,1]$); two retention rates ($\beta_s \in [0,1]$ and $\beta_f \in [0,1]$), two generalization functions ($g_s \in [0,150]$ and $g_f \in [0,1]$), and the proportion of learning in each system that transfers from training to generalization ($\gamma_s \in [0,1]$ and $\gamma_f \in [0,1]$). We obtained best-fitting parameter estimates by minimising the sum of squared error difference between the observed endpoint hand angles and the model predictions:

$$E = \sum_{t=1}^{N_{trials}} \left[\boldsymbol{x}_{pred,t} - \boldsymbol{x}_{obs,t} \right]^2$$
 (15)

To find the parameter values that achieved this minimum, we used the differential evolution optimisation method implemented in *SciPy*. To construct 95% confidence intervals of the resulting parameter estimates, we created a bootstrapped estimate of the sampling distributions of each parameter. In particular, for each experiment and condition containing *N* participants, we sam-

pled N participants with replacement, computed the average endpoint hand angle per trial collapsing over subjects (denoted by x^*), and found the model parameters that minimised the sum of squared error between the model predictions and the bootstrap sample average:

$$E^* = \sum_{t=1}^{N_{trials}} \left[x_{pred,t} - x^*_{obs,t} \right]^2$$
 (16)

We then repeated this procedure 10,000 times. 95% confidence intervals were constructed for each parameter estimate by taking the 2.5 and 97.5 percentile values from the bootstrap estimated sampling distribution.

Results

Figure 2A and 2C show the mean hand angle across all participants per group for each trial of the experiment. Figure 2B and 2D show the generalization pattern for each group.

Baseline motor performance

First, we assessed group differences in baseline motor performance. For all movement parameters (RT, MT, PV, HA), we performed ANOVAs for the within-subject factors of TARGET (11 target directions) and CONDITION (feedback vs no-feedback), and the between-subject factor GROUP (experts vs controls). While there was a significant effect of GROUP, no GROUP × TARGET, or GROUP × TARGET × CONDITION interactions were observed indicating no differences across target directions or feedback conditions during the baseline phase (1).

Hand angles during baseline were normally distributed (Shapiro-Wilk test; Controls baseline: p=.229; Experts baseline: p=.383; Controls adaptation: p=.133; Experts adaptation: p=.208). Experts were on average more accurate. Error (rotation - hand angle) was smaller for experts ($mean \pm SE = 1.1 \pm 0.053^{\circ}$) than for controls ($4.0 \pm 0.127^{\circ}$) (p < .001, d=0.66). Experts were also more precise (exhibited lower variance) in their movement endpoints compared to controls (Levene's test for equality of variances F(1,3958) = 1041.94, p < .001). RT was shorter on average ($350 \pm 180ms$) for experts than for controls ($480\pm200ms$) (p < .001, d=0.61), and MT was shorter on average ($760 \pm 135ms$) for experts than for controls ($900 \pm 180ms$)(p < .001, d=0.795). However, peak

velocity was greater for controls ($PV = 15.2 \pm 7.2 cm/s$) than experts ($14.4 \pm 6.5 cm/s$) (p < .001, d = -0.105).

Visuomotor adaptation

We then tested whether the rate and extent of visuomotor learning during the adaptation phase differed between experts and controls. We performed a repeated measures ANOVA on HA for the within-subject factor of BIN (10 trials per bin), the interaction between BIN × GROUP, and the between-subject factor of GROUP across 11 bins. There was a significant within-subject effect of BIN ($F_{1,10} = 59.6, p_h <$ $.001, \omega^2 = 0.213$), which indicates that hand angles in both groups changed over time in response to the rotation. There was also a significant interaction between BIN × GROUP ($F_{1.10} = 14.4, p_h < .001, \omega^2 =$ 0.058), reflecting that experts compensated for the rotation more quickly than controls. The effect size for both comparisons was small. A significant between-subject effect of GROUP ($F_{1,1} = 269, p_h < .001, \omega^2 = 0.573$), indicating an overall difference in hand angle between groups. This effect size was more appreciable.

Group differences were present in the first two bins (Experts adapted 73.7% (21.5 \pm 6.3 deg) compared to 62.9% (17.1 \pm 5.5 deg) for controls (p < .001; baseline adjusted)), but not significant in the last two bins (Experts adapted 98.7% (29.6 \pm 2.0 deg) compared to 94.9% (28.5 \pm 4.3 deg) for controls (p < .923; baseline adjusted)), indicating that experts differed from controls initially, but that performance between the groups ultimately reached similar asymptotic levels.

Generalization

Finally, we investigated whether spatial generalization of learning differed between the groups (Figure 3B and 3D show the generalization pattern for each group). As with the adaptation results, we first performed a repeated measures ANOVA. The within-subject factor of TARGET and TARGET x GROUP interaction, as well as the between-subject factor of GROUP, were compared across the 11 targets (6 trials per target). There was a significant within-subject effect of TARGET ($F_{1,9.67} = 2518.2, p_h < .001, \omega^2 = 0.95$ Greenhouse-Geisser corrected) indicating that adaptation generalized to different extents across target direction. There was also a significant TARGET x GROUP interaction

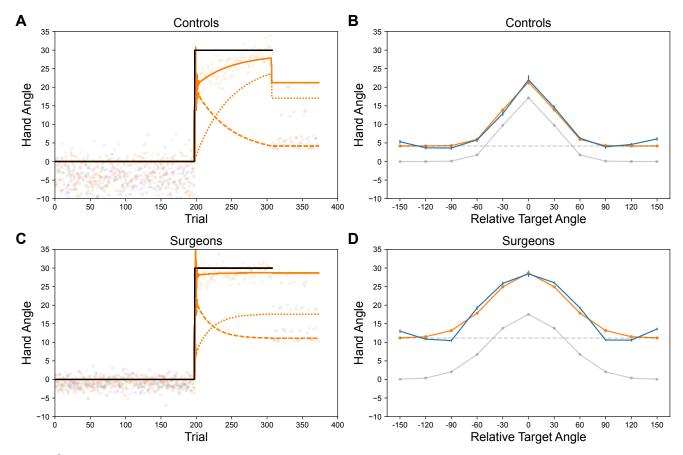


Figure 2. A: Mean handle angles for controls. B: Generalization for controls. Colored dots correspond to different targets. The solid line is the total output of the best-fitting state-space model, the thick-dashed line is the output of the fast system, and the thin-dashed line is the output of the slow sytem. C: Mean hand angle for surgeons. D: Generalization for surgeons. Blue, orange, grey-solid and grey-dashed lines represent behavioural data, model fit, g_s and g_s respectively.

| | GROUP | GROUP × TARGET | $GROUP \times TARGET \times CONDITION$ |
|----|---|------------------------------|--|
| RT | $F_{1,1} = 331.1, p_h < .001, \omega^2 = 0.077$ | $F_{1,1}0 = 1.218, p = .274$ | $F_{1,1}0 = 1.04, p_h > .99$ |
| MT | $F_{1,1} = 564, p_h < .001, \omega^2 = 0.124$ | $F_{1,1}0 = 1.137, p = .331$ | $F_{1,1}0 = 1.14, p_h > .99$ |
| | | $F_{1,1}0 = 0.91, p = .523$ | |
| HA | $F_{1,1} = 394.5, p_h < .001, \omega^2 = 0.091$ | $F_{1,1}0 = 0.752, p = .675$ | $F_{1,1}0 = 0.831, p_h > .99$ |

Table 1 Baseline phase performance statistics. p_h indicates the Holm-Bonferroni corrected p-value.

 $(F_{1,9.67}=130.8,p_h<.001,\omega^2=0.496;$ Greenhouse-Geisser corrected), indicating that experts generalized more broadly than controls. The between-subject effect of GROUP was also significant $(F_{1,1}=12276,p_h<.001,\omega^2=0.990;$ Greenhouse-Geisser corrected), indicating that experts' pattern of generalization across targets was different from controls.

State-Space Modelling

We also performed state-space modelling (see methods). The predicted performance from the best fitting model is shown in Figure 3. Figure 3 shows the best-fitting value, along with the bootstrap estimated sampling distributions for each model parameter.

For all statistical results reported below, we used a bootstrap t-test. The difference in best fitting parameter values between experts and controls was significant for both retention parameters [$\beta_s : p < .05; \beta_f : p < .01$],

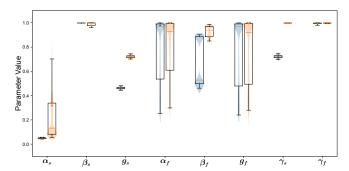


Figure 3. Bootstrap estimated sampling distributions for every parameter in the fitted models. Control data is blue, Expert data is orange.

with experts displaying higher retention in the fast system and lower retention in the slow system than controls. This indicates that experts came to rely on their fast system relatively more than controls, while controls came to rely on their slow system relatively more than experts. The slow system generalization width parameter was also significantly different between groups $[g_s: p < .01]$, with experts generalizing more broadly than controls. Finally, the slow system context transfer parameter was also significantly different between experts and controls [γ_s : p < .01], reflecting that – upon transfer to the generalization phase - experts retained essentially all of their adaptation from training, whereas controls lost a significant portion. Visual inspection of Figure 2 shows that both experts and controls display a positive uniform shift in their generalization, and this is reflected in our best-fitting g_f values for these two groups, which are both significantly different from zero (see Figure 3). However, the difference in this shift – which appears greater for experts than for controls was not statistically significant $[g_f: p = .98]$. No other between-group difference in parameters was significant $[\alpha_s: p = .09; \alpha_f: p = .80; g_f: p = .98; \gamma_f: p = .16].$

One of most interesting aspects of our data is that control performance drops precipitously from the end of adaptation to the generalization phase, and expert performance does not (as reflected in the statistical difference in best-fitting context transfer parameters γ_s). Inspection of Figure 3 indicates that this difference must be driven though the slow system, and shows that differences in γ_f cannot capture this results.

Discussion

In the current study, we hypothesized that expert minimally invasive surgeons would exhibit enhanced visuomotor learning compared to controls either because they draw on an extensive body of experience coping with such visuomotor perturbations, are inherently more adept at compensating for visuomotor perturbations, or both. During minimally invasive procedures an assistant typically directs the camera through one of the ports on the opposite side of the patient to the surgeon, and must often adjust the camera position and orientation to improve the view of the operative field. This means that the visual feedback the surgeon uses is often rotated and/or translated. Importantly, every rotation and translation of the camera is a visuomotor perturbation in the sense that the mapping between surgical movements and visual feedback is altered (i.e., the same motor commands will not lead to the same visual outcome). These considerations were the basis for our predictions about enhanced visuomotor performance among expert surgeons.

Surprisingly little attention has been given to surgeons as an informative expert cohort in visuomotor learning studies. More generally, there has been limited exploration of group-level differences in visuomotor adaptation [24],[36]. In the most relevant study to date, Leukel and colleagues [24] explored visuomotor learning in expert handball players. Similar to our study, they reported lower task-relevant movement variability (higher consistency) and greater accuracy in their expert group prior to learning, both widely considered to be hallmarks of expert performance [37]. Yet interestingly, they observed no learning rate differences in one experiment and a slower rate of adaptation in experts compared to novices in another experiment. One plausible explanation for this discrepancy is that handball players do not have to contend with or achieve mastery over changes in visuomotor mappings as do expert surgeons with extensive training and experience performing MIS. However, other differences between their study and ours make precise comparisons difficult.

State-space model is more than curve-fitting

Our analysis in this paper leans heavily on a twostate state-space model that was simultaneously fit to all phases of our experimental data. Specifically, the fitting routine was constrained to simultaneously find a single set of parameters that best fit the pattern of reach endpoints observed during baseline, adaptation, and generalization. As such, our model departs from more traditional curve-fitting approaches including fitting exponential or power functions to adaptation data and Gaussian functions to generalization data. It also differs from state-space modelling approaches that fit only a subset of data at a time (e.g., using one set of parameters to fit adaptation and another to fit generalization).

Group differences during adaptation are driven by retention rate, not learning rate

In a standard visuomotor adaptation task, we found that expert minimally invasive surgeons compensate for visuomotor perturbations more rapidly than naive controls, but to an equal extent. To shed light on possible drivers of this effect, we developed a computational model that assumed that visuomotor adaptation is driven through the combination of two learning systems or processes - one that is fast and labile, and another that is slow and stable [32]. This model explicates several factors that could make experts compensate more successfully than controls, the most intuitive of which is that experts adapt more in response to experienced errors (i.e., experts might have a larger learning rate then controls). Our modelling results reject this hypothesis, although there was a trend in this direction (e.g., a onetailed test for α_s being larger for experts than for controls was significant at p<.05). This suggests that there may in fact be real learning differences between groups, but that our study may have been under-powered.

Another possibility is that experts might exhibit more stable adaptation than controls (i.e., they might have a larger retention rate than controls). Our modelling results strongly suggest that this is the case, but the exact mechanism must be considered carefully. In particular, relative to controls, experts had more stable adaptation in the fast system, but less stable adaptation in the slow system. The net effect of this arrangement is that experts came to rely on their fast system more than controls, and controls came to rely on their slow more than experts.

This pattern seems especially relevant in light of theoretical considerations that associate the fast system with explicit strategies, whereas the slow system is associated with implicit motor adaptation. By this view, during adaptation, experts come to rely on explicit strategies proportionally more than controls, while controls come to rely on implicit motor adaptation more than experts. Thus, the difference in compensation during adaptation might indicate that experts simply aim better than controls.

Difference in generalization width

We found that (1) both groups exhibited generalization functions that were approximately Gaussian with peaks at the trained target direction, (2) experts generalized more broadly than controls, and (3) both groups displayed a positive uniform shift of the entire Gaussian shape significantly greater than zero. Our modelling shows that this uniform shift in hand angles across target directions can be naturally accounted for by assuming that the fast system corresponds to explicit aiming, and that it generalizes uniformly, as suggested by previous literature [34,35].

If the deployment of explicit strategies is the primary driver of group differences in our generalization results (e.g., as implied by the retention rate differences discussed above), then we would expect a larger positive shift in the generalization curve of experts but not an increase in the width of the Gaussian, the latter of which is presumably driven by implicit motor adaptation. However, our results indicate the opposite of this prediction. The uniform shift in the generalization function caused by the fast system (g_f) did not significantly differ between groups. Thus, experts and controls appear to have generalized the use of strategies similarly. Furthermore, the width of the Gaussian generalisation curve was significantly different between groups, as seen for example in best-fitting g_s values, and this likely reveals a true difference in implicit motor learning for experts as compared to controls. It remains to be determined whether broader spatial generalization is a benefit or cost to expert MIS surgeons. On one hand, it could help surgeons cope with visuomotor perturbations that remain relatively stationary during a procedure such as when camera position is held constant relative to the workspace. On the other hand, over-generalisation may lead to interference when perturbations are highly variable such as when the camera position needs to be adjusted repeatedly to obtain a suitable view of the workspace.

Transfer cost in controls, but not experts

We observed a large difference between groups in the best fitting context transfer parameter, η_s . This difference is reflected in the pronounced drop-off from training to generalization for controls, but not in the surgeons. Note that Figure 2 shows that the drop in hand angle from training to generalization seen in the controls very likely cannot be driven by the fast system context transfer parameter, η_f , because no between-group difference in η_f ever occurred in 10,000 bootstrap samples. Thus, the cost of transferring from training to generalization appears to be a property of the slow system (i.e., implicit motor learning).

Transfer costs like the one displayed by our control group are common. A sharp drop in error compensation between the end of adaptation and the start of a no-feedback (washout/de-adaptation) phase of between $\sim 20\%$ to $\sim 40\%$ has been previously observed [38],[16], [39], [40], [41], [42]]. From this perspective, it is remarkable that our expert group did not display any transfer cost. Thus, this appears to be another difference in the implicit visuomotor adaptation system of experts.

Explanations based on general motor performance

We found that during baseline reaches, experts were more precise, exhibiting lower variance in their movement endpoints compared to controls. However, these general characteristics of motor performance cannot account for the results observed during adaptation and generalization. First, all individual adaptation data for both experts and controls were baseline corrected so that any possible effects of greater accuracy among surgeons (or higher error among controls) were factored out in our results. Second, changes in variance should not appreciably change the reported means in our data since our baseline and adaptation endpoint data are normally distributed according to a Shapiro-Wilk test for normality (see Results). Finally, recent work exploring the link between intrinsic motor variability and motor learning ability [43] generates predictions that run counter to what we observed. Wu et al. [44] report that participants exhibiting higher levels of baseline motor variability tended to express faster adaptation rates compared to individuals with lower motor variability. Since surgeons show lower intrinsic motor variability

(defined in our paradigm as lower variance in hand angle during the baseline phase) than controls, this would predict slower not faster, motor learning. Again, this is not what we observed.

Group differences in reaction time (RT) or total movement time (MT) also cannot explain our visuomotor learning results. First, consider RT. Although the relationship between changes in RT and visuomotor adaptation has received relatively little attention, there is some evidence for a correlation [45]. Specifically, participants who exhibited the largest RT increases during early stages of visuomotor adaptation to a visuomotor perturbation showed the fastest learning rates, whereas participants who incurred little or no RT cost exhibited slower learning rates. This is not what we observed. In our study, control participants showed longer RTs and slower learning rates on average during the adaptation phase, whereas expert surgeons showed shorter RTs and faster learning rates on average. Fernandez-Ruiz et al. (2011) [46] attributed the longer RTs to participants' deployment of a cognitive strategy (i.e., mental rotation), which is known to exhibit a time cost [47],[48]. Based on this interpretation, our findings would suggest that it is controls rather than experts who more extensively exploit explicit strategies. However, this is not what is indicated by our generalization results.

Next, consider MT. Based on Fitts' law [49], which characterizes an inverse relationship or "tradeoff" between movement time and spatial accuracy, the faster overall movements of experts should be associated with lower accuracy and the slower overall movements of controls should be associated with higher accuracy. However, this is not what we observed. Experts exhibited higher spatial accuracy (lower error) during the baseline phase than controls. No significant interactions between MT and HA or RT and HA were found during baseline or adaptation phases.

Explanations based on attention do not account for our results

Certain expert cohorts have been shown to have enhanced attentional capacities [48,49], and this has even been directly linked to improvements in visuomotor adaptation [50]. It is therefore possible that the observed differences in performance in our study reflect attentional differences between surgeons and controls. Yet specific features of our paradigm make this expla-

nation unlikely. Even if the surgeons we tested have superior attentional capacities compared to controls, our task is not very attentionally demanding – only a single reach target is presented per trial without the appearance of any distractors. Although attention has been shown to affect generalization of visuomotor learning [51],[52], these studies use concurrent attention-demanding secondary tasks during the adaptation period which differs substantially from the paradigm we employed.

Explanations based on age do not account for our results

Finally, age differences between the groups (median age of controls = 23; median age of surgeons = 45) do not account for the observed results. Studies investigating the effect of age on visuomotor adaptation consistently report a negative correlation between the ability to compensate for a visuomotor rotation and age in healthy adult populations [43], [53], [54], [55], [56], yet our results show the inverse result. That is, the older experts compensated for the perturbation better than younger controls.

Limitations

The current study has several important limitations. First, although our findings indicate that the visuomotor learning abilities of expert surgeons differs from naive controls, our study does not address whether these differences are innate or reflect extensive experience training for and performing minimally invasive surgeries under visuomotor perturbations (or some combination of both). Appropriately designed longitudinal studies or different cross-sectional studies involving one or more intermediate groups between surgical experts and naive controls will be required to tackle this critical issue.

Second, this study does not fully tease apart the relative contribution of implicit learning versus explicit strategy use [32], [33], [57], [58]. Although some of our results suggest that experts and controls are similar with respect to their use of cognitive strategies such as explicit changes in aiming, it remains possible that some expert-level differences may be revealed through additional experiments. Experiments specifically designed to decompose the contributions of these different learning processes such as those involving explicit aim-

ing [58], [59], constrained movement preparation time [60], [61], and/or the inclusion of a discrete washout (de-adaptation) phase to probe for after-effects [32] will be required to make progress on this issue [33], [57], [58]. We hope that the current findings provide the impetus for this important future work.

Conclusions

Despite its major benefits for patients compared to open surgery, it is now widely recognized that minimally invasive surgery is inherently challenging to learn and can even be prohibitively difficult for some surgical residents such that they never reach proficiency [48], [62]. Pinpointing the underlying sources of these difficulties remains an unanswered challenge. The main findings reported here of expert-level differences in visuomotor adaptation suggest that differences in visuomotor learning capacities, either innate or acquired, might be an important source of difficulty for learning to perform minimally invasive surgery. Because our study demonstrates that a standard visuomotor learning paradigm gives rise to reliable task performance differences between expert minimally invasive surgeons and non-experts, this opens the door for the exploration of other common paradigms such as gain adaptation [21], which may in turn shed valuable light on motor learning and expert performance in increasingly dominant approaches in surgical medicine such as robotic surgery.

References

- [1] Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error Correction, Sensory Prediction, and Adaptation in Motor Control. *Annual Review of Neuroscience*, *33*(1), 89–108. doi:10.1146/annurev-neuro-060909-153135
- [2] Krakauer, J. W. [John W], & Mazzoni, P. [Pietro]. (2011). Human sensorimotor learning: Adaptation, skill, and beyond. *Current Opinion in Neurobiology*, 21(4), 636–644. doi:10.1016/j. conb.2011.06.012
- [3] Cuschieri, A. (1995). Whither Ilfinimal Access Surgery: Tribulations and Expectations. *The American Journal of Surgery*, *169*, 9–19.

- [4] Braga, M., Vignali, A., Gianotti, L., Zuliani, W., Radaelli, G., Gruarin, P., ... Carlo, V. D. (2002). Laparoscopic Versus Open Colorectal Surgery. *Ann. Surg.* 236(6), 9.
- [5] den Boer, K., de Jong, T., Dankelman, J., & Gouma, D. (2001). Problems with Laparoscopic Instruments: Opinions of Experts. *Jour*nal of Laparoendoscopic & Advanced Surgical Techniques, 11(3), 149–155. doi:10.1089/ 10926420152389297
- [6] Joice, P., Hanna, G., & Cuschieri, A. (1998). Ergonomic evaluation of laparoscopic bowel suturing. *The American Journal of Surgery*, 176(4), 373–378. doi:10.1016/S0002-9610(98)00202-5
- [7] Wentink, B. (2001). Eye-hand coordination in laparoscopy an overview of experiments and supporting aids. *Minimally Invasive Therapy & Allied Technologies*, 10(3), 155–162. doi:10.1080/136457001753192277
- [8] Rattner, D. W. (1999). Beyond the laparoscope: Minimally invasive surgery in the new millennium. *Surgery*, 4.
- [9] Schauer, P., Ikramuddin, S., Hamad, G., & Gourash, W. (2003). The learning curve for laparoscopic Roux-en-Y gastric bypass is 100 cases. *Surgical Endoscopy*, 17(2), 212–215. doi:10.1007/s00464-002-8857-z
- [10] Prinz, W., Beisert, M., & Herwig, A. (2013). Action science: Foundations of an emerging discipline. *MIT Press*.
- [11] Heuer, H., & Sülzenbrück, S. (2013). Tool Use in Action: The Mastery of Complex Visuomotor Transformations. In W. Prinz, M. Beisert, & A. Herwig (Eds.), *Action Science* (pp. 36–62). doi:10.7551/mitpress/9780262018555.003.0002
- [12] Pouget, A., & Snyder, L. H. (2000). Computational approaches to sensorimotor transformations. *Nature Neuroscience*, *3*(S11), 1192–1198. doi:10.1038/81469
- [13] Soechting, J. F., & Flanders, M. (1989). Errors in pointing are due to approximations in sensorimotor transformations. *Journal of Neurophysiology*, 62(2), 595–608. doi:10.1152/jn.1989.62.2.595
- [14] Sober, S. J., & Sabes, P. N. (2005). Flexible strategies for sensory integration during motor planning. *Nature Neuroscience*, 8(4), 490–497. doi:10.1038/nn1427

- [15] Cunningham, H. A. (1989). Aiming error under transformed spatial mappings suggests a structure for visual-motor maps. *Journal of Experimental Psychology: Human Perception and Performance*, 15(3), 493.
- [16] Krakauer, J. W. [John W.]. (2009). Motor Learning and Consolidation: The Case of Visuomotor Rotation. In D. Sternad (Ed.), *Progress in Motor Control* (Vol. 629, pp. 405–421). doi:10.1007/978-0-387-77064-2_21
- [17] Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. doi:10.1016/0028-3932(71)90067-4
- [18] Gozli, D. G., Bavelier, D., & Pratt, J. (2014). The effect of action video game playing on sensorimotor learning: Evidence from a movement tracking task. *Human Movement Science*, *38*, 152–162. doi:10.1016/j.humov.2014.09.004
- [19] Lynch, J., Aughwane, P., & Hammond, T. M. (2010). Video Games and Surgical Ability: A Literature Review. *Journal of Surgical Education*, 67(3), 184–189. doi:10.1016/j.jsurg.2010. 02.010
- [20] Li, L., Chen, R., & Chen, J. (2016). Playing Action Video Games Improves Visuomotor Control. *Psychological Science*, 27(8), 1092–1108. doi:10.1177/0956797616650300
- [21] Krakauer, J. W. [John W.], Pine, Z. M., Ghilardi, M.-F., & Ghez, C. (2000). Learning of Visuomotor Transformations for Vectorial Planning of Reaching Trajectories. *The Journal of Neuro*science, 20(23), 8916–8924.
- [22] Krakauer, J. W. [John W.], Ghilardi, M.-F., & Ghez, C. (1999). Independent learning of internal models for kinematic and dynamic control of reaching. *nature neuroscience*, 2(11), 1027.
- [23] Brayanov, J. B., Press, D. Z., & Smith, M. A. (2012). Motor Memory Is Encoded as a Gain-Field Combination of Intrinsic and Extrinsic Action Representations. *Journal of Neuroscience*, *32*(43), 14951–14965. doi:10.1523/JNEUROSCI.1928-12.2012
- [24] Leukel, C., Gollhofer, A., & Taube, W. (2015). In Experts, underlying processes that drive visuomotor adaptation are different than in Novices.

- Frontiers in Human Neuroscience, 9. doi:10. 3389/fnhum.2015.00050
- [25] Georgopoulos, A., Kalaska, J., Caminiti, R., & Massey, J. (1982). On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *The Journal of Neuroscience*, 2(11), 1527–1537. doi:10.1523/JNEUROSCI.02-11-01527.1982
- [26] Scott, S. H., Gribble, P. L., Graham, K. M., & Cabel, D. W. (2001). Dissociation between hand motion and population vectors from neural activity in motor cortex. *Nature*, *413*(6852), 161–165. doi:10.1038/35093102
- [27] Holm, S. (1979). A Simple Sequentially Rejective Multiple Test Procedure. *Scand J Statist*, 6, 65–70.
- [28] Thoroughman, K. A., & Shadmehr, R. (2000). Learning of action through adaptive combination of motor primitives. *Nature*, *407*(6805), 742–747. doi:10.1038/35037588
- [29] Cheng, S., & Sabes, P. N. (2006). Modeling Sensorimotor Learning with Linear Dynamical Systems. *Neural Computation*, *18*, 760–793.
- [30] Wolpert, D. M., Miall, R., & Kawato, M. (1998). Internal models in the cerebellum. *Trends in Cognitive Sciences*, 2(9), 338–347. doi:10.1016/S1364-6613(98)01221-2
- [31] Poggio, T., & Bizzi, E. (2004). Generalization in vision and motor control. *Nature*, *431*(7010), 768–774. doi:10.1038/nature03014
- [32] Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting Adaptive Processes with Different Timescales Underlie Short-Term Motor Learning. *PLoS Biology*, *4*(6), e179. doi:10. 1371/journal.pbio.0040179
- [33] McDougle, S. D., Ivry, R. B., & Taylor, J. A. (2016). Taking Aim at the Cognitive Side of Learning in Sensorimotor Adaptation Tasks. *Trends in Cognitive Sciences*, 20(7), 535–544. doi:10.1016/j.tics.2016.05.002
- [34] Heuer, H., & Hegele, M. (2011). Generalization of implicit and explicit adjustments to visuomotor rotations across the workspace in younger and older adults. *Journal of Neurophysiology*, 106(4), 2078–2085. doi:10.1152/jn.00043.2011
- [35] McDougle, S. D., Bond, K. M., & Taylor, J. A. (2017). Implications of plan-based generaliza-

- tion in sensorimotor adaptation. *Journal of Neurophysiology*, *118*(1), 383–393. doi:10.1152/jn. 00974.2016
- [36] Kast, V., & Leukel, C. (2016). Motor Experts Care about Consistency and Are Reluctant to Change Motor Outcome. *PLOS ONE*, *11*(8), e0161798. doi:10.1371/journal.pone.0161798
- [37] Willingham, D. B. (1998). A Neuropsychological Theory of Motor Skill Learning. *Psychological Review*, *105*, 558–584.
- [38] Hinder, M. R., Walk, L., Woolley, D. G., Riek, S., & Carson, R. G. (2007). The interference effects of non-rotated versus counter-rotated trials in visuomotor adaptation. *Experimental Brain Research*, 180(4), 629–640. doi:10.1007/s00221-007-0888-1
- [39] Sadnicka, A., Patani, B., Saifee, T. A., Kassavetis, P., Pareés, I., Korlipara, P., ... Edwards, M. J. (2014). Normal Motor Adaptation in Cervical Dystonia: A Fundamental Cerebellar Computation is Intact. *The Cerebellum*, *13*(5), 558–567. doi:10.1007/s12311-014-0569-0
- [40] Haar, S., Donchin, O., & Dinstein, I. (2015). Dissociating Visual and Motor Directional Selectivity Using Visuomotor Adaptation. *Journal of Neuroscience*, 35(17), 6813–6821. doi:10.1523/JNEUROSCI.0182-15.2015
- [41] Jalali, R., Chowdhury, A., Wilson, M., Miall, R. C., & Galea, J. M. (2018). Neural changes associated with cerebellar tDCS studied using MR spectroscopy. *Experimental Brain Research*, 236(4), 997–1006. doi:10.1007/s00221-018-5170-1
- [42] Nakagawa-Silva, A., B. Gouveia, E., & B. Soares, A. (2018). A FRAMEWORK FOR VISUOMOTOR ADAPTATION STUDIES. In Anais do V Congresso Brasileiro de Eletromiografia e Cinesiologia e X Simpósio de Engenharia Biomédica. doi:10.29327/cobecseb.78868
- [43] Anguera, J. A., Reuter-Lorenz, P. A., Willingham, D. T., & Seidler, R. D. (2011). Failure to Engage Spatial Working Memory Contributes to Age-related Declines in Visuomotor Learning. *Journal of Cognitive Neuroscience*, 23(1), 11–25. doi:10.1162/jocn.2010.21451
- [44] Wu, H. G., Miyamoto, Y. R., Castro, L. N. G., Ölveczky, B. P., & Smith, M. A. (2014). Tempo-

- ral structure of motor variability is dynamically regulated and predicts motor learning ability. *Nature Neuroscience*, *17*(2), 312–321. doi:10.1038/nn.3616
- [45] Anguera, J. A., Reuter-Lorenz, P. A., Willingham, D. T., & Seidler, R. D. (2010). Contributions of Spatial Working Memory to Visuomotor Learning. *Journal of Cognitive Neuroscience*, 22(9), 1917–1930. doi:10.1162/jocn.2009.21351
- [46] Fernandez-Ruiz, J., Wong, W., Armstrong, I. T., & Flanagan, J. R. (2011). Relation between reaction time and reach errors during visuomotor adaptation. *Behavioural Brain Research*, 219(1), 8–14. doi:10.1016/j.bbr.2010.11.060
- [47] MacKenzie, I. S. (1995). Movement Time Prediction in Human-Computer Interfaces. In *Readings in Human-Computer Interaction* (pp. 483–493). doi:10.1016/B978-0-08-051574-8.50050-9
- [48] Green, C. S., & Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature*, 423(6939), 534–537. doi:10.1038/nature01647
- [49] Bavelier, D., & Green, C. S. (2019). Enhancing Attentional Control: Lessons from Action Video Games. *Neuron*, *104*(1), 147–163. doi:10.1016/j.neuron.2019.09.031
- [50] Debats, N. B., & Heuer, H. (2018). Explicit knowledge of sensory non-redundancy can reduce the strength of multisensory integration. *Psychological Research*. doi:10.1007/s00426-018-1116-2
- [51] Bedard, P., & Song, J.-H. [J.-H.]. (2013). Attention modulates generalization of visuomotor adaptation. *Journal of Vision*, *13*(12), 12–12. doi:10.1167/13.12.12
- [52] Wang, T. S. L., & Song, J.-H. [Joo-Hyun]. (2017). Impaired visuomotor generalization by inconsistent attentional contexts. *Journal of Neu*rophysiology, 118(3), 1709–1719. doi:10.1152/ jn.00089.2017
- [53] Seidler, R. D. (2006). Differential effects of age on sequence learning and sensorimotor adaptation. *Brain Research Bulletin*, 70(4-6), 337–346. doi:10.1016/j.brainresbull.2006.06.008
- [54] Voelcker-Rehage, C. (2008). Motor-skill learning in older adults—a review of studies on age-

- related differences. *European Review of Aging and Physical Activity*, *5*(1), 5–16. doi:10.1007/s11556-008-0030-9
- [55] King, B. R., Fogel, S. M., Albouy, G., & Doyon, J. (2013). Neural correlates of the age-related changes in motor sequence learning and motor adaptation in older adults. *Frontiers in Human Neuroscience*, 7. doi:10.3389/fnhum.2013.00142
- [56] Buch, E. R. (2003). Visuomotor Adaptation in Normal Aging. *Learning & Memory*, 10(1), 55– 63. doi:10.1101/lm.50303
- [57] Mazzoni, P. [P.]. (2006). An Implicit Plan Overrides an Explicit Strategy during Visuomotor Adaptation. *Journal of Neuroscience*, 26(14), 3642–3645. doi:10.1523/JNEUROSCI.5317-05.2006
- [58] Taylor, J. A. [J. A.], Krakauer, J. W., & Ivry, R. B. (2014). Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *Journal of Neuroscience*, *34*(8), 3023–3032. doi:10.1523/JNEUROSCI.3619-13.2014
- [59] Bond, K. M., & Taylor, J. A. [Jordan A.]. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of Neuro-physiology*, *113*(10), 3836–3849. doi:10.1152/jn.00009.2015
- [60] Haith, A. M., Huberdeau, D. M., & Krakauer, J. W. (2015). The Influence of Movement Preparation Time on the Expression of Visuomotor Learning and Savings. *Journal of Neuroscience*, 35(13), 5109–5117. doi:10.1523/JNEUROSCI. 3869-14.2015
- [61] Leow, L.-A., Gunn, R., Marinovic, W., & Carroll, T. J. (2017). Estimating the implicit component of visuomotor rotation learning by constraining movement preparation time. *Journal of Neurophysiology*, *118*(2), 666–676. doi:10.1152/jn.00834.2016
- [62] Buckley, C. E., Kavanagh, D. O., Nugent, E., Ryan, D., Traynor, O. J., & Neary, P. C. (2014). The impact of aptitude on the learning curve for laparoscopic suturing. *The American Journal of Surgery*, 207(2), 263–270. doi:10.1016/j.amjsurg.2013.08.037